ESSAYS IN GEOBOTANY
IN HONOR OF
WILLIAM ALBERT SETCHELL

William A. Setchell

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EDITED BY

T. H. GOODSPEED

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Editorial Preface

In 1934, the Editorial Committee of the University of California approved a proposal to issue a volume in honor of Professor Setchell, who, in 1935, after forty years of active participation in the life and work of the University, would become seventy years of age and Professor of Botany Emeritus. The editor was authorized to request articles dealing with the subject of the proposed book from distinguished botanists in this country and abroad. The magnitude of the editorial task which proved to be involved, together with certain unforeseen circumstances causing delays, have made it necessary that this anniversary volume appear post festum. *The editor is under great obligation to the various authors for their interest and coöperation, to Dr. Helen-Mar Wheeler, and to the editorial staff of the University of California Press for much assistance and advice.*

Since the material in this volume brings together authoritative statements concerning the status of the various problems of geobotany, its usefulness as a text for advanced students and as a book of reference should be considerable.

T. H. GOODSPEED, EDITOR.

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WILLIAM ALBERT SETCHELL

A Biographical Sketch

By T. H. Goodspeed

William albert setchell was born on April 15, 1864, in Norwich, Connecticut. Remotely of Danish ancestry, the Setchell family came to America from the North Coast of England in late Colonial or early Revolutionary times. They intermarried with the old Standish, Case, and Jans families, whose American beginnings were still older. His mother was born in England of English-Welsh parents, and came to America as a small child. He is, therefore, of a decidedly American descent which involved English, Dutch, and Welsh ancestry.

From his earliest years, Professor Setchell exhibited a decided predilection for "natural history." As a small child, among other pursuits in this domain, he sought attractive and interesting plants from which he would pull portions and plant them, to be replaced, when faded, with others. This and other evidence of interest in plants ultimately attracted the attention of the family physician, who, when the boy was nine or ten years old, gave him a copy of Mrs. Lincoln's *Botany for Young Ladies,* which contained a species of manual arranged on the Linnean system. Therewith he puzzled out the names of many plants and made a beginning in systematics which cannot have failed to leave its mark, particularly since the labor involved in these first steps stimulated rather than dampened his enthusiasm for plant study. It was further aroused (in 1876) by a journey with his parents and his grandmother to Philadelphia and the Centennial Exposition, with stops in New York City and elsewhere;

he saw to it that visits were made to botanical gardens and conservatories, and to zoölogical gardens and aquaria besides.

When he was sixteen and a student in Norwich Free Academy, the curriculum there included a course in Gray's *Lessons in Botany* in which some attempt was made at determining species. The young man showed so lively an interest that he was asked to assist in collecting material for the class. He was also given special privileges; he could leave the classroom to follow his own desires in plant collecting, or pursue independent study in the botanical section of the school library. There is perhaps an indication here that the "project method" in secondary education had its champions even before the present generation of schoolmasters! His collecting enthusiasm was paralleled by that of George R. Case, Deputy Collector of Internal Revenue in the Norwich District, with whom Professor Setchell became acquainted about this time. Together they proposed the preparation of a local flora to include all plants found within a radius of ten miles from the center of the city of Norwich, the species to be determined by Gray's *Manual* and to be arranged in order of flowering. In this last proposal appears the background of a research interest which was to engage Professor Setchell's efforts many years later. Finally, in 1883, the list of Norwich plants was published. Of further significance in this early period of Professor Setchell's botanical experience was his discovery of the fern *Aspleneum montanum* some hundreds of miles west of its previously known range, an event which was communicated to Professor Daniel Cady Eaton of Yale University. The appearance of his first scientific contribution, together with the enthusiasm engendered by a botanical discovery, led the young man to consider himself somewhat established in a botanical career.

When, in 1883, he entered Yale University, there was almost no instruction offered in botany, at least not to members of the classical course in Yale College. However, Professor Eaton, having some acquaintance with him as a result of the fern discovery and appreciating his botanical ardor, opened the way. He admitted him to his home, where, as Professor Setchell writes, "I occupied a table in a corner of his combined library, herbarium, and study room, a large and magnificent room with mantelpieces carved to represent certain North American fern species. A good library, a good herbarium, and a very sympathetic instructor!" Various factors in this stimulating and satisfying environment went far in determining Professor Setchell's future botanical inclinations as well as broadening his immediate botanical horizon. For a year or two he had been collecting seaweeds, and the presence of W. E. Safford in New Haven encouraged this pursuit. Safford, then an ensign in the United States Navy, had obtained leave to study the marine algae under Eaton. Setchell and he immediately combined forces and soon began to make progress in their joint phycological studies. At the same time, he became acquainted with a fellow student, J. B. Hatcher, who was then studying the Hepaticae. Hatcher, who was graduated soon after Setchell's freshman year, obtained an appointment in the United States Geological Survey and was sent to Kansas to engage in paleontological field work. For two or three years he collected representatives of the plains flora, sending his specimens to Setchell, and with Eaton's aid, Setchell determined them. His work on this material, containing, as it did, genera and species almost all of which were new to him, made the first considerable contribution to Setchell's knowledge of the morphology and taxonomy of vascular plants and of the factors which influence their distribution.

His earliest contact with what was to become his major research interest came about 1880, when he made a series of visits to the seashore in Eastern Connecticut and collected marine algae. The algae were named according to the information contained in Hervey's *Sea Mosses,* and the phycological experience thus derived was supplemented by the later association with Eaton and Safford, already referred to. An important influence which during this early period further stimulated Professor Setchell's growing enthusiasm for algology was an acquaintanceship, made through Eaton, with Mr. Isaac Holden, of Bridgeport, Connecticut. He was Vice-President and Business Manager of the Wheeler and Wilson Sewing Machine Company, and spent his week ends and holidays in exploring the seashore and studying his collections. While Setchell was at Yale, and later when he was at Harvard, Holden and he collected and studied together and ultimately formulated a project which was to be realized some years afterward when they associated with themselves another amateur phycologist, Mr. Frank S. Collins, of Malden, Massachusetts. In the absence of any manual of North American algae, and because they were not then in a position to prepare one, they proposed to issue series of mounted and named specimens which would make available to the interested public the products of their collections and studies. The ultimate result was the preparation of 51 fascicles of the *Phycotheca-Boreali-Americana* (1895–1919), which distributed to correspondents throughout the world some 200,000 specimens and which represent a collection that will always be fundamental in investigations of the algae of North America.

To the triumvirate who gained for the *Phycotheca-Boreali-Americana* its initial success there was added, during Professor Setchell's early years in Berkeley, N. L. Gardner, another phycologist who at the beginning had amateur status only. In 1897, Gardner, then a school teacher in Coupeville, Whidbey Island, Washington, submitted to Professor Setchell his collections of seaweeds from the Puget Sound region, an area which had not been explored for marine algae in more than fifty years, and where Gardner found unusually large numbers of new or little-known species. The scientific and later personal and professional relation thus established between Professors Setchell and Gardner continued during the latter's undergraduate years at the University of Washington and preparation for the doctorate at Berkeley. For many years as colleagues at the University of California they have collaborated in the preparation of a series of monographs, intended ultimately to cover the algal flora of the Pacific Coast.

In his senior year at Yale, Professor Setchell had decided to continue his studies in cryptogamic botany, as an avocation at least. The question of a vocation, which had necessarily to be answered soon, resolved itself in his mind into a choice between becoming a teacher of the classics in preparatory schools, taking up the profession of medicine, or attempting to carry on his botanical studies to the point where he might hope to obtain a university appointment. This third alternative, although attractive, seemed to him least likely of success until, on the recommendation of Eaton and with the aid of W. G. Farlow, he obtained an appointment as a Morgan Fellow in Harvard University to pursue studies in both botany and zoölogy.

Professor Setchell's period of graduate study at Cambridge (1887–1890) was replete with those broadening and refining influences, scientific and cultural, which today, because of early specialization and the administrative and curricular pressure upon faculty and students, are so rarely available to the graduate student in most American universities. In Farlow's laboratory he was associated particularly with Kingo Miyabe and W. C. Sturgis. Both of them were more advanced in their studies than he, but they worked with him sympathetically. Among his fellow students in Mark's laboratory were G. H. Parker, H. H. Field, C. B. Davenport, H. B. Ward, C. H. Eigenmann, and C. W. Woodworth. These friends, together with advanced students in other fields—including John Manley and E. B. Delabarre—formed a most stimulating group. Besides their attachment to the natural sciences, they shared an enthusiasm for literature, painting, and music. They attended concerts and lectures, and visited the Boston Museum of Fine Arts; and their discussions in the laboratory were not restricted to scientific topics. The refinement of Professor Setchell's taste, the breadth and quality of his literary background, and his interest in and knowledge of the fine arts are referable, in part at least, to these Harvard experiences superimposed upon his early training in the classics.

During the two years following, at Cambridge, Professor Setchell served as an assistant in biology and held a proctorship. As proctor, he had to do with matters of discipline in the college dormitories and with the conduct of examinations. At the beginning of the second year he was granted the degree of Master of Arts, the only requirements for which were to request its conferment and to submit evidence of a proper record in course work. Since the assistantship permitted him only half-time for his graduate studies, he found it necessary to give up the research in zoölogy which he had begun under Mark and to give himself exclusively to the thesis topic under Farlow. The problem decided upon for the thesis concerned the morphology and development of *Saccoriza dermatodea,* a characteristic kelp of the northern New England coasts. In the meantime, a certain small group of fungi, the *Doassansia* group, had aroused in him a new and keen interest, stimulated by his having obtained the germination of curious spore masses or sori. Farlow frowned upon this new enthusiasm as tending to occupy time better spent upon research on the thesis topic. Nevertheless Professor Setchell succeeded in continuing the *Doassansia* work by carefully apportioning the morning hours in the laboratory: until 9:30 he concerned himself with *Doassansia,* thereafter with *Saccoriza,* and thus was always engaged upon the latter when Farlow made his daily round.

Together with fellow students in the laboratory, Professor Setchell was encouraged to call occasionally in the evening at Farlow's bachelor apartments. On these occasions the professor regaled the group with anecdotes having to do with the personalities and work of many botanists, living and dead. By this means Professor Setchell acquired an extensive though somewhat unassorted mass of information on botanical history and, more, an enduring interest in the subject. Many years later, a result of this manifested itself in the preparation of a semester of lectures entitled "The History of Botany." This was the first organized course in the undergraduate curriculum at the University of California which dealt exclusively with the historical development of a biological field. For many years it was deservedly popular with students of other disciplines besides the biological.

In 1890, Professor Setchell obtained the doctorate, and a year later accepted appointment as an assistant in botany in Yale University. Soon thereafter he began to consider, among other problems in the marine algae, the distribution of the kelps, and presented his preliminary conclusions before the Connecticut Academy of Science in a short paper entitled, "Geographical Distribution of the Laminariaceae." In the discussion which followed, questions were raised concerning the factors which had brought about the distribution of certain marine algae, and in particular, the possible importance of the temperature factor was discussed. Here, then, was the origin of a point of view which Setchell has effectively developed. Indeed, one of his most significant research contributions has had to do with the establishment of critical temperature intervals in relation to the distribution of the algae and, more recently, of other aquatic plants and of terrestrial plants. With respect to the algae, for example, he has shown that an interval of 5° C. in amplitude determines the zone of distribution of a species, and the seasonal invasion of these zones by members of other zones.

Five years later, Professor Setchell was called to the University of California to become Professor of Botany and Chairman of the Department, an appointment which he held continuously until his retirement as Professor Emeritus in 1934. He was one of those younger men whom Benjamin Ide Wheeler brought to Berkeley to assist him in the building of the greater university—an institution which will never cease to reflect the foresight and wisdom of one who was perhaps the greatest of the older school of American university presidents. Among Professor Setchell's older associates on the faculty were Joseph LeConte, Hilgard, Rising, and Hesse, and among the younger, Ritter, Leuschner, Louderback, and Blasdale. Under E. L. Greene, his predecessor, the Department of Botany included Marshall A. Howe as an instructor, and as assistants W. L. Jepson, Ivar Tidestrom, and J. Burtt Davy. Later, W. J. V. Osterhout and H. M. Hall became members of the staff. For many years, by virtue of his position as head of the Department of Botany, Professor Setchell acted as Botanist of the California Agricultural Experiment Station. In 1898, there was erected a small building provided with laboratories and certain herbarium space, and this was occupied by the department for more than thirty years—indeed, until all biological units were housed in the Life Sciences Building.

Over a period of forty years, Professor Setchell has significantly contributed to the life of the University of California. At the beginning he had much to do with the organization of the greater university. He served on administrative and faculty committees, and was one of those who interpreted the academic atmosphere and traditions of Harvard and Yale in terms of Western ideals and aspirations. Of special importance to the University was the experience he had acquired in his years as a proctor at Cambridge, in dealing effectively and sympathetically with undergraduates. For many years he was both official and unofficial adviser to members of the student body, and their appreciation was expressed by his early election to membership in their honor societies. In his official capacity he assisted in the formulation of the then unique system of student self-government, suggested and fostered by President Wheeler and perpetuated by later administrations, which has been adopted by so many institutions of collegiate and lesser grade as one of the surest means of developing individual and group loyalty and responsibility among undergraduates. In his unofficial capacity he still continues to act *in loco parentis* to many young men and particularly to those in whom he sees promise, and in many parts of the world his former students and foster children acknowledge their indebtedness to him for the guidance, encouragement, and assistance—often material assistance—which he so wholeheartedly offered them in their college days.

Setchell's scientific contributions reflect a remarkably wide range of interests, some having their origin in the influences and environment which were part of his biological training and which have already been mentioned, others being referable to influences which have operated more recently, and still others being somewhat incidental products of circumstance. Certain of his diverse research concerns represent fields which he plowed and later passed on for cultivation to colleagues and students. Soon after coming to Berkeley, Setchell met Dr. H. W. Harkness, President of the California Academy of Sciences, who had long studied the subterranean or hypogaeous fungi, and who desired assistance in preparing his observations for publication. This incidental meeting revived Setchell's interest in the fungi which had had its beginning in Farlow's laboratory, and as a result he has been engaged for many years with the aid of N. L. Gardner, Helen M. Gilkey, Lee Bonar, and H. E. Parks, in assembling representative collections of California species. Though the fungi herbarium and its study have been turned over to Professor Bonar, these collections still enlist his interest. Later on, in the Botanical Garden, of which he was Director for many years, the possibility of growing for instruction and display a collection of the commercial varieties of the tobacco plant and other species of *Nicotiana* led to the obtaining of seed from foreign as well as domestic sources. The early trials of this seed indicated so much confusion with respect to nomenclature that he began to give serious thought to the situation. Rather extensive garden cultures soon produced a series of stable and correctly named species and varieties and, in addition, evidence that the races of commercial tobacco represented hybrid combinations. For some years Setchell gave up his summers to an analysis of varietal hybrids in *Nicotiana Tabacum* and to the results of hybridization among members of the collection of other species which he now had available. From these early studies is derived the extended research program dealing with the cytogenetics of the genus *Nicotiana* which for many years has been carried on by R. E. Clausen, the writer, and their students. In these illustrations of Setchell's more or less incidental research interests are revealed a scientific curiosity and an enthusiasm which were so balanced by a sense of values that profitable ventures have been assured to inheritors of these projects.

In 1920 came what proved to be a major influence upon his career, in an invitation from the Carnegie Institution of Washington to carry on certain investigations in the Samoan Islands. From this beginning there was derived a sustained interest in a variety of Polynesian problems—the building up of coral reefs, the origin of insular floras, the biological as well as the geological history of the crustaceous corallines, ethnobotany—and from it, too, have come his important contributions concerning the paleogeography of the Pacific area. In the following ten years he made a series of journeys in this area, and brought back extensive collections from Hawaii, Tahiti, Tonga, Fiji, Australia, New Zealand, Japan, and South Africa. His undergraduate training in the systematics of vascular plants formed the background for an accumulating knowledge and experience in this field which enabled him to collect with discrimination the significant elements of the Pacific floras with which he came into contact. From these expeditions he acquired first-hand knowledge of the geographic and geologic as well as of the floristic features of the Pacific area in their relation primarily to the fundamental concepts of plant distribution involved. A large place in his thinking today is occupied by these matters, and by his continued investigation of the factors which have brought about the distribution of the marine algae. It is therefore not inappropriate that this volume which honors his scientific achievements should be concerned with geobotany.

Soon after his coming to California in 1895, Setchell undertook an exploration of the West Coast of North America, looking toward a complete treatment of its algal flora. This project has continued to be his major research concern for more than forty years. His phycological contributions, and particularly his monographic treatment, in collaboration with N. L. Gardner, of numerous groups of Pacific Coast algae, have to do with a field in which he was a pioneer and which he has cultivated assiduously and successfully. Early in this work he visited on more than one occasion those European herbaria in which he could familiarize himself with types in the algae. At the same time, he collected extensively from California to Alaska and, on his first journey around the world, in 1903–1904, collected and studied new or little-known algal floras. The broad character of the background thus acquired, together with research enthusiasm matched by industry, a rare sense of morphological values, and a mature judgment, are reflected in the fullness of his phycological contributions and their critical quality. Relieved of teaching and administrative duties as Professor Emeritus, Setchell is increasing his productivity. At present he is engaged, among other things, upon the monographing of certain large genera of the algae, such as *Sargassum* and *Codium,* and of various genera of the Balanophoraceae; consideration of climatological relations of the Wallacean area; and studies of the morphology, taxonomy and, particularly, the distribution of the genus *Zostera.*

In 1920 he married Mrs. Clara B. Caldwell, of Providence, Rhode Island. Mrs. Setchell immediately endeared herself to his colleagues and other friends by her tact, dignity, and sympathetic reaction to her new environment. In a quiet and unpretentious fashion she entered into the life of the laboratories, coming each day to assist her husband, first in the organization and classification of his library, notes, and collections, and later, having perfected herself in microtechnique, in the researches which he had in progress. During the next fifteen years, Mr. and Mrs. Setchell undertook together a series of extended scientific expeditions, principally in the Pacific area. They both enjoyed travel, and in this as in every other aspect of their life together, they found nothing but experiences of mutual interest. Mrs. Setchell's unselfishness and serenity of spirit were never more apparent than during the more than two years of disability which preceded her final illness, and her obvious desire that her condition should as little as possible interfere with the progress of her husband's work was realized.

In this brief biographical statement no effort has been made to recite the total of Professor Setchell's scientific concerns or achievements. Nevertheless, by illustration and comment the breadth of his biological horizon and the importance of his research contributions have, hopefully, been exhibited. An obvious effort has been made throughout to indicate the character of the associations and influences which have operated in initiating and directing his scientific pursuits. Given those qualities of mind which he possesses, certain, at least, of the diverse influences which are sure to approach the biologist may be productive of the broader, more significant, and more useful type of scientific career and should, therefore, not be thrust aside without due consideration. If a somewhat personal tone appears as characteristic of some parts of this effort to present a sketch of a distinguished man, it must be referred to the writer's intimate acquaintance with him for more than a quarter-century.

Among the thirty scientfic societies and other organizations of which Professor Setchell is at present a member, the National

Academy of Sciences, American Philosophical Society, American Academy of Arts and Sciences (Fellow), California Academy of Sciences (Fellow), Washington Academy of Sciences, Torrey Botanical Club (Fellow), Linnean Society of London, Société de Biographie, Société Linnéenne de Lyon, Société pour l'Etudes Océaniennes (Fellow), American Anthropological Association, American Geographical Society, American Association for the Advancement of Science (Fellow, and Past Vice-President, Section G—Botany), Phi Beta Kappa, Sigma Xi, Alpha Zeta, Phi Sigma (Past National President), Alpha Epsilon Sigma, Author's Club (London), Bohemian Club (San Francisco), represent some of those which have honored his scientific achievements and include certain others which indicate the range of his contacts, scientific and otherwise.

THE PRINCIPAL JOURNEYS AND EXPEDITIONS OF W. A. SETCHELL

1896. Expedition during the summer by wagon from Berkeley to the Santa Cruz Mountains, California, through the San Joaquin Valley to Yosemite National Park, and back to Berkeley (with W. L. Jepson)—collections of vascular plants, fungi, and fresh-water algae.

1898. Yellowstone National Park—investigation of thermal algae.

1899. Expedition to Alaska and the Bering Sea (with L. E. Hunt, W. L. Jepson, and A. A. Lawson)—studies of marine algae and general cryptogamic collecting.

1900. Summer in Hawaii (with L. E. Hunt)—studies of marine algae and ethnobotany.

1903–1904. First sabbatical leave from the University of California. Around the world eastward from Berkeley by way of Philadelphia, Europe, Egypt, India, New Zealand—herbarium studies, investigation of marine algae and thermal algae, and general collections.

1908. Summer in European herbaria—study of types in the algae.

1911. European herbaria—study of types in the algae.

1920. Summer in Tutuila, Samoan Islands—investigation of the origin and development of coral reefs, studies in ethnobotany, general collecting.

1922. Summer in Tahiti (with H. E. Parks and Mrs. Clara B. Setchell)—further investigation of the origin and development of coral reefs and problems of plant distribution in the Pacific area, general collecting.

1924. Summer in Hawaii (with Mrs. Clara B. Setchell)—further investigation of coral reefs and distributional problems.

1926–1927. Second journey around the world, westward from Berkeley (with Mrs. Clara B. Setchell). Tonga (with H. E. Parks, J. E. Hoffmeister, and J. M. Ostergaard), Fiji, Samoa, Hawaii, Japan, Australia, New Zealand, South Africa—continuation of earlier studies of problems of the Pacific area; collections of marine algae, general collections.

1929. To Java and the Pan-Pacific Congress, Great Barrier Reef of Australia, and Rarotonga (with Mrs. Clara B. Setchell)—collections of tropical marine algae, general collections.

1931. Summer in Alaska (with Mrs. Clara B. Setchell)—taxonomic and distributional studies of the genus *Salix*.

1932. Summer in Alaska and journeys on the Yukon (with Mrs. Clara B. Setchell)—continuation of *Salix* studies.

The Rate of Plant Migration

By O. W. Arrhenius

In the skerries (small islands) along the east coast of Sweden the migration of plants plays a great rôle. Every year the land rises from about 0.3 to 1.5 cm. New areas are constantly wrested from the sea, and thus the water level in the soil changes from year to year. Consequently the changes in the plant associations are very great, and the rate of migration is important in the formation of the new associations.

Usually these skerries are small—one acre or less. Their highest parts are rocks washed clean by the waves. Between these rocks, in sheltered places, we find the soil apt for vegetation. The most common profile of a place covered with vegetation in the younger skerries is shown in figure 1.

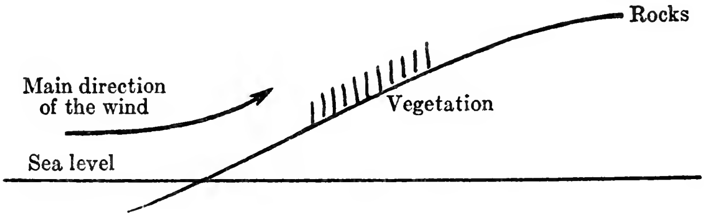

Fig. 1.

In order to examine these and related questions, some "bare areas" were laid out in the early summer of 1920. The areas were prepared as follows. In a typical plant association, a frame of 1 square meter divided with iron strings into 100 small squares was laid out. The plants were counted separately in each small area. After this the humus layer was dug away. The upper part of the mineral soil was then removed, put through a fine sieve, and replaced. The humus also was sieved and replaced on top of the mineral soil. The corners of the area were marked with poles.

This bare area, of course, had not the same properties as the old soil; many of the factors were changed in one direction or the other.

These areas were visited in 1922, 1924, and 1932.

The district of these investigations belongs to the most arid region of Sweden. The annual rainfall is low—from 300 to 400 mm. The moisture of the air is rather high, but the evaporation is strong because of the hard and everlasting winds. The water is the dominating factor.

Tables 1 to 6 (below) present the results of the investigations.

The figures give the real numbers of the plants in each square meter. As a plant the section between the soil and a stem has been counted. When it is possible and of interest, the location of the different plants is given on a map. This shows the number of plants of different species in every small square. The explanation of the signatures is found in the tables; for example, V5 in table 1 marks 5 *Vaccinium vitis idaea.*

From the tables, we see that the plant migration is going on very slowly, especially where the soil is dry. The most extreme condition we find in table 3, where the plants have not succeeded in establishing themselves after twelve years.

Most interesting to see, however, is *how* the migration goes on.

The migration has always taken place from the border. It is those squares which are situated next to the old vegetation which show new vegetation. And where the areas are subject to a prevailing wind—from the shore—we see that the migration chiefly has taken place from the windward side.

The long-distance migration must be of very small importance in these associations.

We may summarize the results as follows. The migration of plants in this district is very slow. The rate of migration is chiefly dependant upon the moisture content of the soil. The chief migration takes place within a very small distance—10–20 cm.—and by the aid of the wind.

TABLE 1

PINUS- CALLUNA- VACCINIUM VITIS-WOOD ON NÄSTHOLMEN—THICK RAW-HUMUS LAYER ON SAND

1920

V2	V1	V1	V1	V1		V1	V1		
V2			V2	V1 C2			V1	V1 C1	V1
V3		C1	V2 C1	V2	C1		V3		
V1	V1		V1	V1	C1	V1		V1	V1
V1	V2	V2	V1	V2	V1	V2	V1 C1	V1	V2
V2	V2	C1	V1	V1	V1	C1	V1	C1	
V2	V2	V1	V1	V1 C1	C3	V2			
V2	V2	C1	V2	V2	V2	V1 C1	V1	V1	C1
V1		V2	V2	V2			V1		
V1	V1 C1	V3	V1 C1	V2	V1	V2	V3 J1	V2	V3

1922

V2	A5								V1
V3									V2
V1									V1
V1									V2
V2									V1
V1									V1
V2									V1
V2									V1
V1	L5		V1	V2 E1		V1	V1	V1	V2
V1 E1	V2	V1 E1	V1	V2 E1	V1	A	10	V1	V2 E1

Plant	1920	1922	1932	Plant	1920	1922	1932
C—Calluna vulgaris	20	....	16	J—Juniperus communis	1	....	....
V—Vaccinium vitis idaea	105	44	136	A—Aira flexuosa	....	15	....
L—Luzula multiflora	....	5	1	E—Empetrum nigrum	....	5	....

TABLE 2—Herbrich Pinus Wood on Munkö

Thick humus on fine sand—Level

1922

			H1		R1	F1		B1	
R1		R1		V1			V1		R1
A1								G1	
C1	V1								Y1
N1									R1
R1	I1								P1
P1									A1
L1									G1
A1		G1							C1
B1	R1		F1	P1	R1	V1	P1	R1	

	1920	1922	1924
V—Vaccinium vitis idaea	398	4	The area covered with a dense vegetation of the same type as the surrounding association
G—Geranium sanguineum	54	3	
F—Fragaria vesca	18	2	
L—Luzula pilosa	20	1	
Melampyrum nemorosum	2	....	
H—Hypochaeris maculata	1	1	
Y—Lathyrus pratensis	10	1	
G—Gnaphalium dioicum	50	....	
B—Galium verum	21	2	
Vicia silvatica	1	....	
Salium boreale	37	....	
R—Rubus saxatilis	4	9	
Chrysanthemum leucanthemum	11	....	
Filipendula hexapetala	9	....	
Solidago virgaurea	38	....	
Festuca ovina	46	....	
Clinopodium vulgare	2	....	
Briza media	3	....	
Sorbus aucuparia	1	....	
Anemone hepatica	1	....	
Linum catharticum	1	....	
I—Viola canina	5	1	
Hieracium pilosella	33	....	
Achillea millefolium	5	....	
Veronica officinalis	42	....	
P—Pimpinella saxifraga	13	4	
Trifolium sp	4	....	
A—Anthoxanthum odoratum	....	3	
N—Angelica silvestris	....	1	
C—Luzula multiflora	....	2	

TABLE 3

ARCTOSTAPHYLUS- PINUS WOOD ON KORSHOLMEN

Raw humus on coarse gravel, very dry

Plant	1920	1922	1932
Arctostaphylus uva ursi	180	....	....
Aira flexuosa	107	....	....
Hieracium sp.	1	....	....

TABLE 4

EMPETRUM-HEATH ON MÅSKÄREN

Mild humus on rather moist sand. The island crowded with seagulls and other birds—Level

Plant	1920	1922	Plant	1920	1922
Empetrum nigrum	160	8	Festuca ovina	....	51
Aira flexuosa	14	74	Sedum acre	....	18
Viola tricolor	6	12	Veronica chamaedrys	....	11
Rumex acetosa	1	28	Galium verum	....	17
Veronica spicata	10	1	Myosotis sp.	....	8
Tanacetum vulgare	3	13	Potentilla anserina	....	9
Stellaria graminea	3	....	Rubus saxatilis	....	6
Rubus chamaemorus	1	....	Valeriana officinalis	....	5
Sagina nodosa	....	180	Draba verna	....	4
			Viola sp.	....	2
Anthoxanthum odoratum	....	70	Allium schoenoprasum	....	1

TABLE 5

MYRTILLUS PICEA- PINUS WOOD ON SKATEN

Thick raw humus on sand and gravel

Plant	1920	1922	Plant	1920	1922
Vaccinium myrtillus	216	5	Melampyrum pratense	12	....
Aira flexuosa	112	....	Calluna vulgaris	3	....
Vaccinium vitis idaea	74	....	Sorbus aucuparia	1	....
Empetrum nigrum	6	4			

TABLE 6

Dry Herbrich Association on Åsmansskäret

Mild humus on sand on the top of the slope. Very dry

1922

X	G2									G3
IX	G3									B1 Y2
VIII	G2									H1 G2
VII	Y2 G1									B2 G2
VI	G2									T1 Y3
V	Y1									H1 G5
IV	T1									B1 G4
III	G1									T1 Y3
II	B1									G2
I	G4	G4 C1	G5 T5 F1	G5 C10 A5	G3 C4 A2 T2	G2 C4 T3	A5 T1 B1	C6 T3		G1

Shore

	1920	1922	1924									
			I*	II	III	IV	V	VI	VII	VIII	IX	X
A Aira flexuosa	919	12	92	39	44	37	35	40	....	....	....	....
G Galium verum	232	53	30	19	13	26	14	36	5	4	6	8
C Clinopodium vulgare	147	25	15	5	4	....	1	....	....	....	....	....
T Tanacetum vulgare	57	16	16	4	1	1	1	1	....	....	....	....
Festuca ovina	19	....	....	....	....	....	....	....	....	....	....	....
F Fragaria vesca	16	1	....	1	2	3	....	1	....	....	....	....
Pimpinella saxifraga	5	....	....	....	....	....	....	....	....	....	....	....
Rumex acetosa	4	....	1	2	....	....	....	....	....	....	....	....
B Arabis hirsuta	3	6	....	....	....	4	6	....	....	....	....	....
Y Hypericum perforatum	1	11	1	....	....	....	....	9	....	....	....	....
Filipendula hexapetala	2	....	....	....	....	....	....	....	....	....	....	....
Scutellaria hastifolia	1	....	7	10	14	7	5	....	....	....	....	....
Veronica spicata	1	....	....	1	....	....	....	....	....	....	....	....
Plantago lanceolata	....	....	....	....	....	....	....	....	....	....	....	....
H Hieracium pilosella	....	2	....	....	....	....	....	....	....	....	....	....
Valeriana officinalis	....	....	....	....	3	....	3	....	....	....	....	....
Draba verna	....	....	....	....	....	2	1	1	....	....	....	....

* The Roman numerals show the rows of small squares as indicated in the map.

The Origin of Crepis and Related Genera, with Particular Reference to Distribution and Chromosome Relationships

By Ernest Brown Babcock

The phyletic relations of the genus *Crepis* cannot be adequately discussed without some consideration of nearly related genera. Although none of these other genera has been as thoroughly studied as *Crepis,* sufficient information is available to indicate rather definitely that the position of *Crepis* with reference to its closest allies is unique. In order to make this clear, it is proposed, first, to review the evidence on comparative morphology, chromosome number, and geographic distribution of these closely related genera so as to present, as clearly as possible in brief and rather general form, a review of this small portion of the *Compositae;* and, second, to summarize the much more detailed information now available concerning *Crepis,* in order to see what further light this may throw on the problem of origin. But, before discussing this group of genera, a few remarks on criteria of relationship may be in order.

This subject has been discussed by the present writer in an earlier publication[1]* in which it was approached from the cytogenetic side. The same general principles that underlie the classification of individual organisms into species must apply *mutatis mutandis* to the classification of species into genera. In other words, just as species are natural groups of individuals, so genera are, or should be, natural groups of species. The criteria of re-

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* Superior figures refer to items in the bibliography at the end of this essay.

lationship which have been used in the present study are comparative morphology, geographic distribution, and chromosome number, size, and morphology, and with respect to certain species additional evidence has been derived from genetic data, especially on interspecific hybrids. The morphological features of greatest usefulness in this group of plants are mentioned below. Like most of the *Compositae,* these species are often difficult to recognize and highly variable or polymorphic. Many of the species which have hitherto been published have had to be revised because they were based on inadequate material or too superficial study of the morphology. The species with which this essay deals have all been carefully reviewed, if described by others, and a number of new species which are included have been so recognized only after critical investigation.

The importance of geographic distribution to the student of plant taxonomy has long been recognized. Studied in connection with the evidence from comparative morphology, the facts of distribution may throw light on the phyletic relations of species as well as of larger groups, and may indicate centers of origin and distribution. Field studies on the variation and ecology of the living plants in nature has also come to be widely appreciated as an invaluable aid in taxonomy. But the individual investigator is definitely restricted in the amount of such work that is practicable, and, in attempting to classify the species in any large, cosmopolitan genus, finds it impossible to apply this method very generally.

In recent years, however, the comparative study of the chromosomes, especially of their number and morphology, has come to be recognized as a useful method of supplementing the evidence from gross morphology and geographic distribution. At the same time, the accumulation of a living collection makes it possible to compare these cultivated species and forms when grown under fairly uniform conditions. Although this can never take the place of thoroughgoing field study, yet it does compensate to a degree for the inability to see the plants growing in the wild. For there is no doubt that the inherent morphological and physiological peculiarities which distinguish species are faithfully reproduced under cultivation, often with an obviousness that is not found in the study of herbarium material alone or even in limited field observations.

In the two decades during which the writer has applied part of his time to the study of *Crepis,* fully half of all the known species have been introduced into cultivation and many of them have been maintained for use in genetical and cytological research extending over a long period. Some of these species have been represented by accessions from many localities throughout the range of distribution, and of others only one or a few accessions have been obtained. Every species in the collection has been examined cytologically, and several reports have been published on the chromosomes in relation to taxonomy and phylogeny in this genus.[2, 3, 4, 17, 21] Meanwhile, the taxonomic literature on the genus has been reviewed and most of the species have been studied critically by the use of herbarium material, at least. In the second part of this paper, the data on geographic distribution in this genus will be summarized and compared with the evidence from chromosome relations with reference to phylogeny. Let us first consider the general aspects of the genus and its position with reference to other most nearly related genera.

CREPIS AND SOME RELATED GENERA

The genus *Crepis* is a natural group of more than two hundred species, being the second largest genus of the subtribe *Crepidinae* of the *Cichorieae,* the tribe which includes all species of the *Compositae* having only ligulate florets in the flowerhead. The largest genus is *Hieracium,* with hundreds of species and thousands of subspecies, varieties, and forms, the constancy of which (at least of many) is made possible by some type of apomictic reproduction. In marked contrast with this condition in *Hieracium* is the nearly complete absence of asexual reproduction in *Crepis.* A few species are stoloniferous and certain others spread from root sprouts, but apomixis is apparently at a minimum and actually has been demonstrated in only one species, *C. tenuifolia,* which is a peculiar species in other respects. (The occurrence of apomixis is also suspected in certain American species with odd chromosome numbers.) Next to *Crepis* in size is *Lactuca,* which in its present vaguely defined state contains between seventy-five and one hundred species. These largest genera, *Hieracium, Crepis,* and *Lactuca,* are well differentiated, although there are borderline species or sections as well as certain small intermediate genera which are discussed below. The other larger genera in the *Crepidinae* are *Chondrilla, Taraxacum, Launea, Sonchus,* and *Prenanthes.* All these but the last are sharply distinguished from the three largest genera. *Prenanthes,* like *Lactuca,* is at present rather vaguely defined. At any rate, both are in need of thorough revision. Nevertheless, for purposes of the present discussion it is possible to deal with them as well-known groups.

These four larger genera, *Crepis, Hieracium, Lactuca,* and *Prenanthes,* include annual, biennial, and perennial herbs, a few of the perennials being somewhat suffrutescent. The earlier leaves usually form a rosette. The flower stems may be simple, scapiform, and merely bracteate, or more or less branched with few or many heads and with the cauline leaves more or less reduced, the uppermost being bractlike. In certain very low or tufted alpine species the flower heads may be few and on very short scapes, or numerous and congested. The heads are large, medium, or small and often many-flowered. The involucre is generally composed of distinct outer and inner series of bracts. The receptacle is naked or shortly ciliate (in two small sections of *Crepis* it is paleaceous). The corolla is tubular below, ligulate above, and 5-dentate. The anther tube and style branches are generally similar throughout except in color and such details as the appendages, and the pappus consists of simple, barbellulate bristles. These are the outstanding resemblances between the five genera. There are, however, numerous differences in the vegetative parts, including the indumentum, also in details of the inflorescence; and differences in the achenes and pappus, in habit, and in color of the flowers are particularly useful for purposes of classification. The differentiation in respect to some of these features has been summarized from the diagnoses of Hoffman,[16] Bentham and Hooker,[5] Robinson and Fernald,[31] and others, and is presented in very general, condensed form in table 1 below.

There are several small genera in the *Crepidinae* which resemble *Crepis* more or less, and no doubt they all deserve careful consideration in any future revision of this subtribe. For purposes of the present discussion, five have been selected which have been merged previously with other genera and all of which, the present writer believes, must be reinstated. It is not the purpose of this discussion, however, to present the complete evidence and formally to propose their reinstatement. They will be used merely as illustrations of the usefulness of the cytological criterion. *Ixeris* Cass. has been included in *Lactuca* by Hoffmann and it is certainly closer to *Lactuca* than to *Crepis,* but in

TABLE 1

Differences Between the Four Largest Genera of the Crepidinae Which Are Most Used in Classification of Species

Genera	Achenes	Pappus	Aggregate inflorescence	Flower color	Indumentum
Crepis	more or less terete, attenuate at summit or beaked, 10–20-ribbed	1–4-seriate, white or yellowish, usually fine and soft	scapose, scapiform, paniculate- or cymose-corymbiform, heads erect in anthesis	yellow, often reddish on outer face, rarely pink or sometimes white in one species	never stellate, mostly short-hairy with or without glands, sometimes setose, sometimes glabrous
Lactuca	more or less compressed parallel to involucre, contracted at summit or beaked, few-ribbed	multiseriate, white or yellowish, fine, soft	paniculate in many forms, heads erect in anthesis	yellow, blue, purple, rarely white	glabrous or setose on lower parts
Hieracium	terete or prismatic, truncate at summit or (some sections) attenuate, mostly 10-ribbed	1-seriate, brown, yellowish or rarely white, coarse, rigid, brittle, rarely fine and soft	scapose, scapiform, cymose-corymbiform or paniculate-racemose, heads erect in anthesis	yellow, orange-yellow, purplish, rarely white	stellate and/or long-hairy on lower parts and/or shortly gland-pubescent
Prenanthes	subterete or somewhat compressed, often 3-5-angled, not beaked, truncate or contracted at summit	2– 3- or multi-seriate, brown, yellow or whitish, coarse, rigid, brittle	racemose, paniculate, or thyrsoid, heads mostly nodding in anthesis	yellow, purple, blue, rose, white	long-hairy throughout or glabrous

the strict sense of Cassini's definition[7] it cannot belong in *Lactuca,* because the achenes are not strongly compressed and they are 10-ribbed, the ribs being equal and often salient or rounded. Hence the present author agrees with Gray[14] and Nakai[23] in their reinstatement of this genus. The genus *Youngia* Cass. is included in *Crepis* by Hoffmann, and it resembles *Crepis* more than it does *Lactuca;* but unfortunately *Youngia* has been made a repository for a number of species which cannot be classified here in the sense of Cassini's definition.[8] Because of the strongly obcompressed marginal achenes and certain other details, *Youngia* Cass., *sensu stricto,* must also stand as a genus intermediate between *Crepis* and *Lactuca.* The genus *Aetheorrhiza* Cass. is monotypic and the species has long been known as *Crepis bulbosa* (L.) Tausch. Because of the imbricate involucre and the peculiar achenes, which are superficially like those of *Crepis* but are actually unique, this genus should be reinstated. Another species to be excluded from *Crepis* is *Paleya oligocephala* Sch. Bip. The multiseriate, imbricate involucre is alone sufficient to bar it from *Crepis, Lactuca, Hieracium,* and *Prenanthes.* As the type species of this genus was *Crepis albida* Vill., the genus has become synonymous with *Crepis.* The only other species that has been published under *Paleya* (*P. billotioides* Sch. Bip.) is also received under *Crepis.* Hence *P. oligocephala* may constitute a monotypic genus. However, its relationships to certain other dubious species await investigation.

In addition to the foregoing, two small genera have been erected by Nakai[23] for the disposition of certain species which he considers neither *Crepis* nor *Lactuca.* They both resemble *Ixeris* in some degree, but one of them, *Crepidiastrum,* is strongly suffrutescent or shrublike and differs in habit, leaf arrangement, and especially in the *Crepis*-like achenes, which are terete and beakless, with 10 fine, rounded ribs. In fact, both involucre and fruits are more like *Crepis* than *Ixeris*. The other genus, *Paraixeris,* also resembles *Ixeris* somewhat, but differs in having the stem much branched, the fruiting heads nodding, and the achenes subcompressed with 14 or 15 narrow, rounded ribs and a short coarse beak. Nakai's contention that these two genera are intermediate between *Crepis* and *Lactuca* may be well founded, but in my opinion they are both nearer to *Crepis* than to *Ixeris* and, as will be shown below, their chromosome number supports this view. At the same time the relations of these two small genera to *Prenanthes* should be investigated, particularly since in both there is a strong habital resemblance to this genus.

We turn now to the cytological evidence. Although the data on chromosome numbers are far from complete, yet something is known about most of these related genera. At present, the basic haploid numbers as known in the four larger genera are: *Hieracium,* 9; *Lactuca,* 8, 9; *Taraxacum,* 8; *Prenanthes,* 9, 8; and in the smaller genera under discussion the numbers are: *Crepidiastrum,* 5; *Paraixeris,* 5; *Chondrilla,* 5; *Ixeris,* 8; *Youngia,* 8; *Paleya,* 8; *Aetheorrhiza,* 9. In *Crepis,* after the exclusion of those species which on morphological grounds belong in other genera, the numbers 8 and 9 do not occur as basic haploid numbers, whereas 5 is a basic number. This indicates a closer relation between *Crepidiastrum, Paraixeris,* and *Crepis* than between *Crepis* and the other excluded genera. Furthermore, all the species of *Ixeris, Youngia,* and *Aetheorrhiza* thus far examined have chromosomes which are definitely smaller than those of most species of *Crepis.*

Thus the chromosomes provide important evidence in support of the delimitation of *Crepis* as outlined above. Cytology has been similarly helpful in determining the proper classification of certain dubious sections of *Hieracium*. The section *Crepidisperma,* in particular, is characterized by having the achenes more or less attenuate toward the summit, as in *Crepis,* and the pappus white as in most species of *Crepis*. Because of these features of fruit and pappus, certain species were originally described as *Crepis,* for example, *C. ambigua* A. Gray. Cytological examination of this plant showed the haploid number to be 9, which is characteristic of *Hieracium* and not of *Crepis,* and it is probable that the other species of this section have the same base number. Thus cytology supports the inclusion of these species in *Hieracium*.

There exists a very puzzling group of high alpine Himalayan plants which have come to be known as the *"Glomeratae"* from the type species, *Prenanthes glomerata* Dcne., although this species and four or five similar ones have long been known as *Crepis*. The evidence from comparative morphology, however, strongly supports Decaisne's original classification in *Prenanthes,* and now it is known that the haploid number of chromosomes in *P. glomerata* is 8, a number not found in *Crepis* except in certain polyploids. For the present, however, this group may be considered as intermediate between *Prenanthes* and *Crepis*.

The occurrence of 5 as a base number in several species of *Chondrilla*[28] raises a special problem concerning the relationship of this genus to *Crepis*. It has long been considered as closest to *Taraxacum* because of the similarly specialized achenes in the two genera. Although the base number for *Taraxacum* is 8, both genera might have sprung from primitive *Crepis* stock. This is only one of many similar problems awaiting investigation.

Without going into further detail concerning the evidence from comparative morphology and cytology, and as a first step merely toward a better comprehension of the natural relationships of the genera under discussion, we may represent their phylogeny somewhat as in figure 1. This arrangement is in general agreement with the natural system worked out by Cassini[9] on the basis of comparative morphology. On the basis of chromosome numbers alone, *Crepis* may not appear to have had a common origin with *Hieracium, Lactuca, Prenanthes,* and most of the other genera which have been examined cyto-

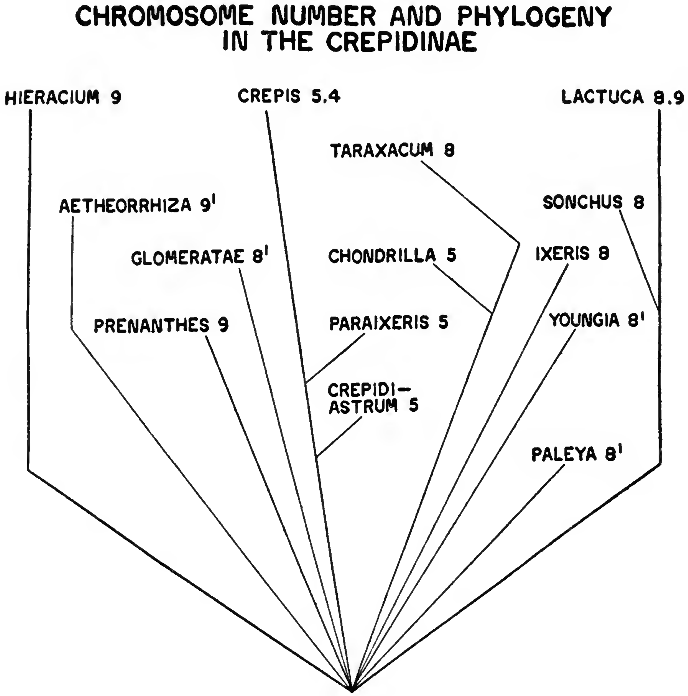

Fig. 1. Chromosome number and phylogeny in the *Crepidinae.*
[1]Only one species reported with respect to chromosome number.

logically. Nevertheless, it does not seem probable that any other genera in the *Crepidinae* will be found to be more closely related to *Crepis* than these. (Two small genera, *Pterotheca* and *Rodigia,* both having 5 as the haploid number, are merged with *Crepis* by the author.) Reference again being made to the evidence from chromosome numbers, the marked divergence of *Crepis, Paraixeris, Crepidiastrum,* and *Chondrilla* from the other genera represented in figure 1, may point to certain evolutionary processes underlying the differentiation of these and perhaps other genera in the *Cichorieae.* As will be shown below, our present knowledge of *Crepis* makes it possible to advance a tentative hypothesis concerning the nature of these processes.

The evidence from geographical distribution supports the conception of a common origin for *Crepis* and its allies. If the distributional areas of the three largest genera are compared, it is found that they all include most of Eurasia and at least part of Africa (fig. 2). All the other genera which have been studied cytologically occur in this same geographical unit. This suggests a common origin for these genera, and the distribution of the more primitive types of *Crepis* and its allies indicates that the region of common origin is south-central Asia. Additional evidence will be presented in the second and third parts of this paper.

The fact that *Hieracium* is so widely distributed might at first seem to indicate that it is therefore the most ancient. But this is not necessarily true, because certain unique features of this great genus are sufficient to explain its present large spread over the earth's surface. According to Zahn,[41] there are numerous species of *Hieracium* which are intermediate between other principal species; these "Zwischenarten" often produce numberless progeny and sometimes considerably transgress the distributional

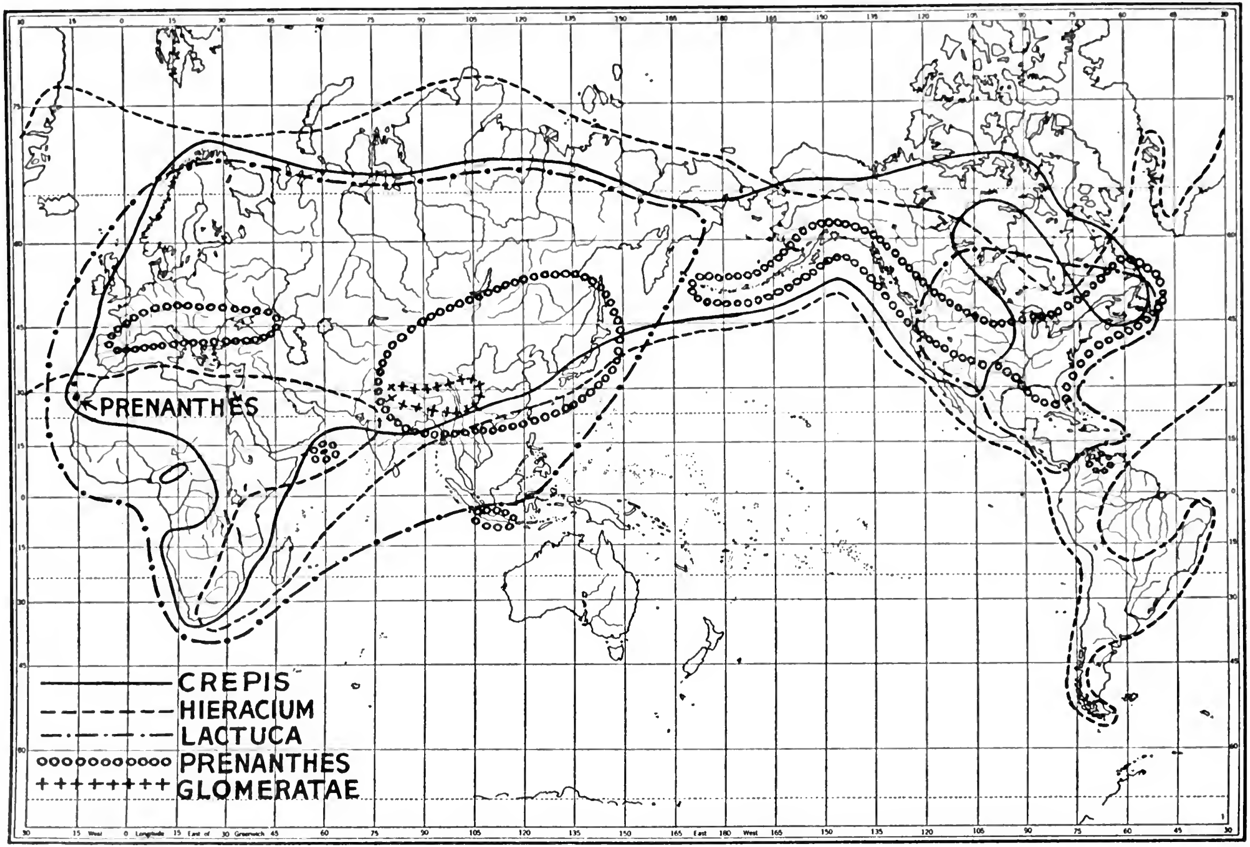

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Fig. 2. General distribution of *Crepis* and four related genera. (But note: for *Prenanthes* see p. 22.)

range of the presumably parental species. In fact, the distribution of Zwischenarten far beyond the range of one or both parents has been frequently observed. Although many of these intermediate species are doubtless hybrids, their distributional dominance is easily explained by the high frequency of apomictic reproduction in this genus. Predominance of interspecific hybrids has been observed in many other genera, but in *Hieracium* it has been an important factor in bringing about the wide distribution of the genus. Undoubtedly another important factor is the usually small size of the achenes, which makes them especially well adapted for wind distribution. In *Crepis,* on the contrary, the fruits of many species, especially the more primitive ones, are larger and heavier and apomixis is almost unknown. Yet the distribution of *Crepis* is nearly as extensive as that of *Hieracium,* the chief difference being that *Hieracium* occupies South America whereas *Crepis* is not known to occur south of northern Mexico. But *Crepis,* even after certain species are excluded, includes some of the most primitive types in the *Crepidinae* (e.g., *C. pontana* and *C. sibirica*). Furthermore, *Crepis* is more widely distributed in Africa than is *Hieracium.* Hence it is probable that *Crepis* represents a progenial stock from which both these genera were derived.

The wide distribution of *Hieracium* in South America and the complete absence of *Crepis* from that continent present a distributional problem calling for more detailed study. A suggestion worth considering is that distributional relations such as these will eventually be found to have a bearing on the concept of continental displacement. Good[13] states that, although there is no satisfactory hypothesis of continental displacement, it is believed that one will be forthcoming and that the geography of the flowering plants will afford important evidence in its support. However, if both genera originated in south-central Asia and migrated into North America by way of a land bridge, even though *Crepis* is the more primitive, a difference in time of migration and the special adaptations of *Hieracium* species for rapid dissemination would explain the present distributional relations of the two genera. Furthermore, the South American species of *Hieracium* having attenuate achenes and fine white pappus must be among the most advanced members of the genus. It is well known that various species of flowering plants in South America are closely allied to North American species and appear to have migrated from north to south.

Lactuca (fig. 2) has a distributional range about as extensive as that of *Crepis* but, in certain morphological features, particularly in specialization of fruits, it appears to be a more advanced group of species. Its extensive geographic range does not necessarily indicate antiquity greater than that of *Crepis*.

Prenanthes is less extensive in distributional range than *Lactuca* (fig. 2), but the evidence from comparative morphology shows that *Prenanthes* is the more primitive. If the distribution of *Prenanthes* be examined in some detail, it will be found to be consistent with the conception that it was formerly more widespread. However, the small areas indicated on the map (fig. 2) in the Canary Islands, Java, South America, and probably Socotra Island may be disregarded. Herbarium studies made since this map was printed indicate that none of these species are of this genus. Nevertheless, both comparative morphology and distribution indicate that *Prenanthes* may be more primitive than *Crepis*.

THE GENUS CREPIS

The genus comprises three subgenera, *Catonia, Eucrepis,* and *Barkhausia,* which are differentiated primarily according to degree of specialization of the involucre and secondarily by the amount of specialization of the achenes. In *Catonia,* as the fruits mature, the involucre merely increases in size and the bracts may become somewhat thicker and indurate but with little, if any, change in shape. In the other two subgenera, the bracts of fruiting heads have a median dorsal keel and become more or less swollen at the base by development of soft spongy tissue. The achenes in *Catonia* and *Eucrepis* are not as a rule provided with a true beak, the slender stipe bearing the pappus, but in *Barkhausia* the beak is always present. There are naturally certain exceptions to these generally reliable distinguishing features, but such exceptional species usually exhibit some marks of resemblance to other species whose subgeneric affinity is clearly marked. In general it is obvious that there is increasing specialization of the involucre and the fruits as one passes from *Catonia* through *Eucrepis* to *Barkhausia.* Along with this increasing specialization there is a definite trend toward reduction in length of life. All the species of *Catonia* are perennials, while about one-fourth of the *Eucrepis* species and three-fourths of the *Barkhausia* species are annuals.

A somewhat similar situation exists in the three subgenera with reference to the proportion and nature of endemic species. Although some species are so rare or poorly represented in herbaria that the extent of their distribution is wholly conjectural, yet the distribution of the majority is sufficiently known to classify them as either restricted to a single geographical unit or of wider extent. In this sense, the proportion of endemics in *Catonia* is about one-half; in *Eucrepis* one-third, and in *Barkhausia* less than one-third of the species are thus restricted. Furthermore, on the basis of relative degree of specialization through reduction in size of plant and its parts, increase in num-

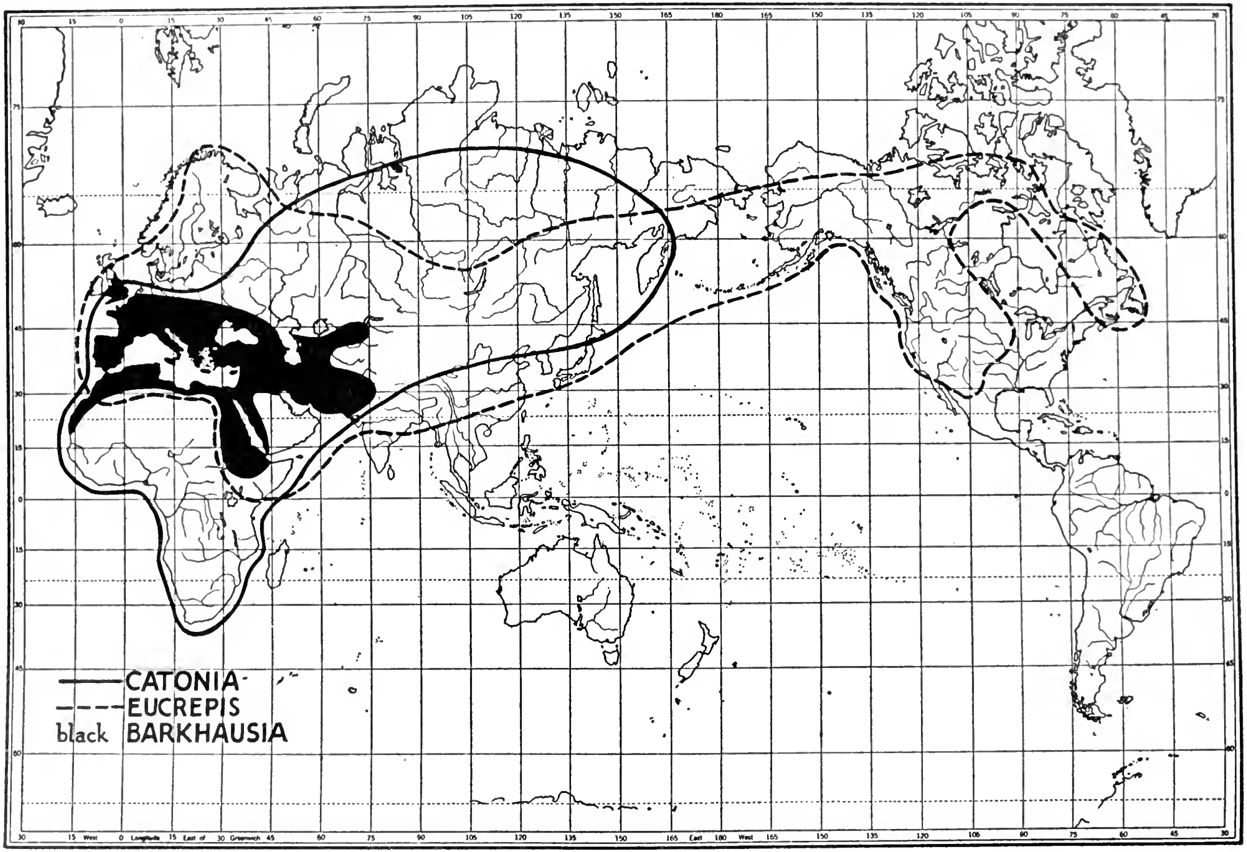

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Fig. 3. Distribution of the three subgenera of *Crepis*.

ber of flower heads, and reduction in length of the life cycle, the endemics can be classified roughly as "old" or "young." The former category obviously includes the more primitive species or relics, and the latter contains the comparatively recent ones. In all three subgenera about one-third of the endemics appear to be old species. Thus the proportions of endemics and of relics in the subgenera is in harmony with the conception that *Catonia* is the most primitive, *Barkhausia* the most recent, and *Eucrepis* intermediate.

The geographical distribution of the subgenera is in general agreement with this conception. As is shown in figure 3, *Catonia* occupies most of Europe, Asia, and Africa, but does not occur in the New World; *Eucrepis* covers about the same area in the Old World except that in Africa it is represented only in the north and northeast, but it is also found in western North America and in a few localities in Labrador and Newfoundland; *Barkhausia* is restricted to the Mediterranean region and adjacent areas. It is significant that *Eucrepis,* which has the widest distribution, contains twice as many species as either of the other subgenera and is more complex in its differentiation into morphologically distinct subgroups. It will be shown below that these evolutionary features are associated with greater variability in chromosome numbers and chromosome morphology in *Eucrepis*. The phyletic relations between the three subgenera are summarized in figure 4.

The somatic chromosome numbers found in the Old World species of *Crepis* are 6, 8, 10, 12, 14 (15–24), 16, and 40, while the North American species have 22, 33, 44, 55 (?), and 88 (?), besides 14 in two representatives of an Old World group. In figure 5 the distribution of these numbers in the subgenera is shown by indicating as exponents the numbers of species known to have certain chromosome numbers. From this representation it is obvious that *Eucrepis* is much more variable in chromosome numbers than the other subgenera.

Although 8 is the most prevalent diploid number in the genus, 10 must be considered more primitive, because the most primitive species in the genus have 10 chromosomes in their somatic cells, and because no species having 10 chromosomes are as greatly reduced or specialized as some of the species having 8. It follows, therefore, that all the 8-chromosome species have been derived from 10-chromosome progenitors; and similarly, the two 6-chromosome species were probably derived from 8-chromosome ancestors. The evolutionary processes involved in such changes have been discussed elsewhere.[2, 4, 17] All numbers higher than 10 are secondary, and have been derived by various processes of which interspecific hybridization and doubling of the whole chromosome complement are of most general importance.

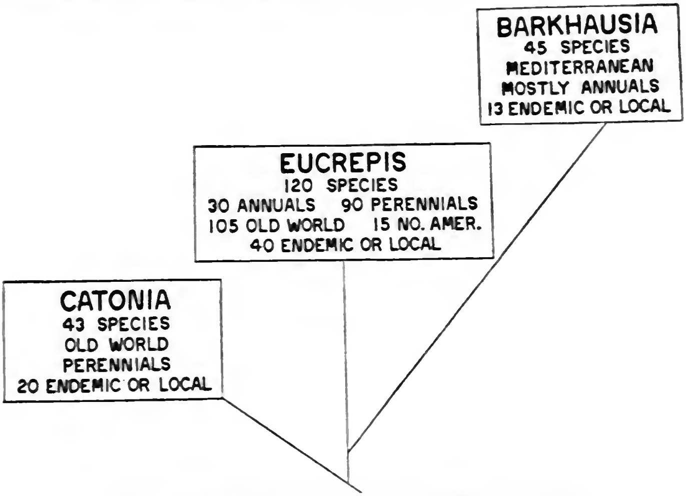

Fig. 4. Phyletic relations of the subgenera of *Crepis*.

Throughout the genus there is close correspondence between chromosome numbers and external morphology of the plants. Although the most primitive species have 10 chromosomes, there are some fairly primitive 8-chromosome types. In both 10-chromosome and 8-chromosome series there is abundant evidence of progressive development from the woody-based perennials with large lyrate or entire leaves, few large heads, large florets, and large unspecialized fruits to the short-lived annual types with small leaves, numerous small heads, small florets, and

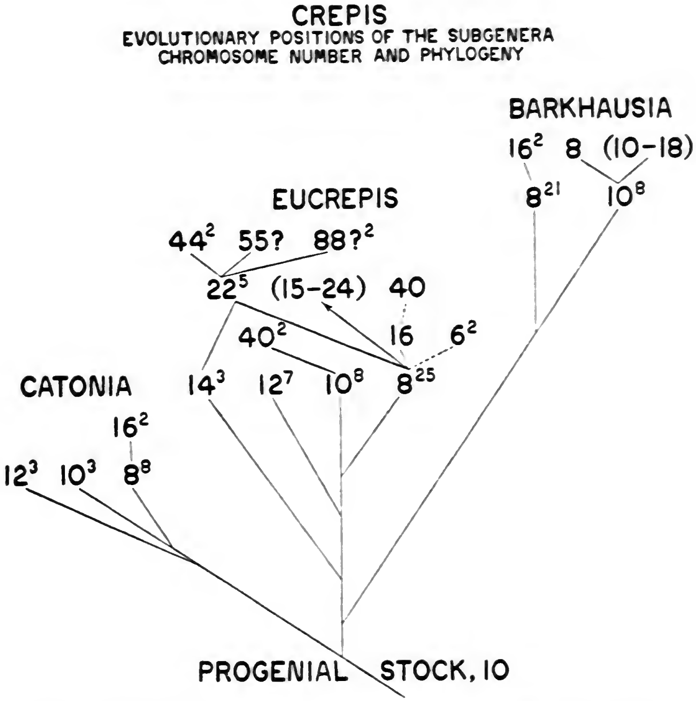

Fig. 5. Distribution of chromosome numbers in the subgenera of *Crepis*.

very small or highly specialized fruits. The basic, primitive diploid number is 10 and there are three 5-paired phylogenetic lines, one in each subgenus. Furthermore, the subgenera are not separated by fixed limits. From the peculiarities of certain species, it is clear that *Catonia* tends to merge into *Eucrepis,* and *Eucrepis* into *Barkhausia.* Hence it seems highly probable that the three 10-chromosome lines, one in each subgenus, had their origin in a common nexus. At any rate, the genus must be accepted as a natural unit.

The chromosomes of *Crepis* species are of three distinct types, namely, those with a subterminal spindle-fiber constriction, those with a subterminal constriction and bearing a trabant or satellite attached to the proximal arm, and those with an approximately median constriction. By comparing total length and relative length of the proximal and distal arms, chromosomes of the first general type are subdivided into classes designated A, B, and C, the satellite-bearing chromosome is called D, and the small median-constricted chromosome, E.[24] One exception to this general scheme occurs in a few species of *Eucrepis* in which the largest chromosome has a median constriction, but there are good reasons for considering this chromosome a modified A type. Every simple diploid species of *Crepis* has only one pair of satellite-bearing chromosomes. This fact alone often makes it possible to recognize secondary or derived species from the regular presence of more than two D chromosomes in the somatic cells, even without a complete analysis of the whole complement.

All the 10-chromosome species of *Crepis* have one pair each of chromosome types A, B, C, D, E. Just as 10 is the most primitive number in the genus, so this combination of five types must be considered the basic genom (haploid complement of a diploid species). All the 8-chromosome species have one pair each of types A, B, C, D. The two 6-chromosome species have one pair each of A, B or C, and D. All species thus far analyzed with numbers higher than 10, have been found to have genoms resulting either from duplication of certain of the types present in the basic genom or from complete doubling of the whole complement. Thus, in the 12-chromosome species, there may be duplication of A, B, C, D, or E and sometimes one type is absent; whereas the 14-chromosome species always have the basic genom plus extra chromosomes of C, D, or E types. This indicates hybrid origin for both the 12- and the 14-chromosome species. Again, all the 16-chromosome species have only A, B, C, and D types and are polyploids derived from 4-paired ancestors. Analysis of distribution of chromosome types in the species with higher numbers has not been completed, but in some of the American species having 22 chromosomes in their somatic cells, the two pairs of D chromosomes are unlike. This strongly indicates that these species originated through interspecific hybridization followed by doubling of both specific complements (amphidiploidy). Similar evidence has been found in two Old World species having 40 chromosomes. Figure 6 illustrates the basic genom of three primitive species, one from each subgenus; and derived genoms with smaller chromosomes and with less and more than 5 are shown.

Chromosome number and morphology are taxonomic criteria of great value in the genus *Crepis,* especially when used in connection with other available criteria. It is certain that morphologically similar species have similar chromosomes and, conversely, close similarity in the chromosomes has often proved to be a helpful clue to a closer degree of relationship than was at first surmised from superficial gross morphology. Thus it has

Fig. 6. Primitive and derived genoms in *Crepis:* left, *Catonia;* middle, *Eucrepis;* right, *Barkhausia.*

been possible to work out with greater accuracy the classification of species into groups within each subgenus, and to ascertain phylogenetic relations. Figure 7 shows the genoms of ten *Eucrepis* species which provide a fine illustration of marked specific differentiation without any gross chromosomal alterations. The five species represented in the left column are perennials, and the others are annuals. Among the perennials, *gymnopus* of Japan, *praemorsa* of Russia, and *incarnata* of southern Europe are more similar to one another morphologically than to *Eigiana* and *Reuteriana* of Syria. The two latter species are closely related, and very different from *palaestina, pulchra,* and *pterothecoides,* which occur in the same region. In fact, the three species last named have in the past been referred to three different genera, *Cymboseris, Phaecasium,* and *Crepis.* Yet comparative morphology reveals the close relationship of *palaestina* and *pulchra,* and establishes that *pterothecoides,* although most precocious and short-lived and very distinct from the other annuals, also belongs in this group. Of the two remaining annuals, *granatensis* is a very close relative of *pulchra* and occurs locally within the range of this widely distributed species, and *Stojanovii,* an endemic of Bulgaria, is quite as distinct as *pterothecoides,* although obviously related to *pulchra.* This group therefore includes widely distributed and highly diversified species, yet the chromosomes throughout are very similar in appearance. Other such groups exist not only in *Eucrepis* but also in both the other subgenera.

These groups of related but well-differentiated species, with very similar chromosomes among the species in each group, are significant in several ways. For one thing, they prove that close similarity in the chromosomes is directly correlated with close taxonomic relationship in *Crepis.* They also indicate that the

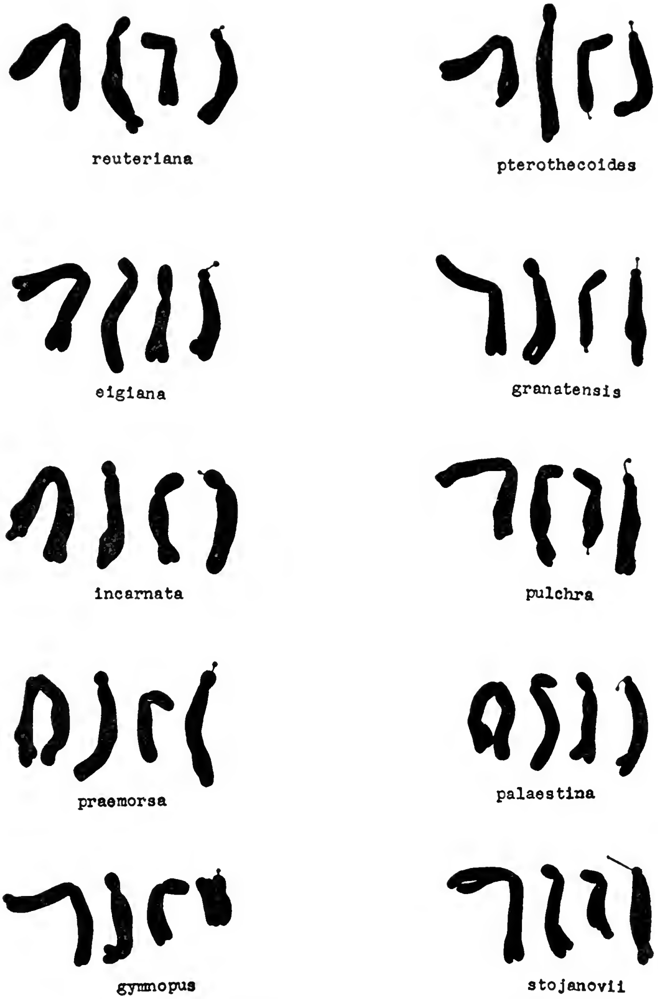

Fig. 7. Haploid complements of a group of closely related but very distinct species of *Eucrepis.*

genetic evolutionary processes involved in speciation within these groups are processes which are not accompanied by many visible changes in the chromosomes. Factor or gene mutation (genovariation) is one such evolutionary process of general occurrence. Experimental genetic evidence is thus far very limited from this group of plants. It can be stated, however, that F_1 hybrids from *C. pulchra* × *C. palaestina* are highly fertile and produce F_2 progeny exhibiting numerous combinations of characters from the original parents. This is just the result that would be expected if the two species differ in numerous genes and yet are homologous with respect to many others. On the contrary, F_1 hybrids from *C. pulchra* × *C. Stojanovii* are nearly if not quite sterile, which suggests an almost complete lack of homology or some combination of genes in the hybrid which prevents sexual reproduction.

Similar evidence from various groups of related species leads to the definite conclusion that gene mutation is an evolutionary process of general occurrence throughout this genus. But it must be viewed as superimposed upon or acting concurrently with those more profound genetic processes involving changes in chromosome number and chromosome morphology.

Changes in size of the chromosomes have occurred in *Crepis* independently of changes in shape. Chromosomes have both increased and decreased in size in the evolution of the genus, but there is a general tendency toward reduction in size of the chromosomes concurrently with reduction in size of the plant and reduction or specialization of parts. In figure 8 the genoms of another group of *Eucrepis* are shown. The differences in size of the chromosomes are striking and they illustrate the general tendency toward reduction in the more recent and highly specialized species. *C. oreades* and *C. Robertioides* are perennials but

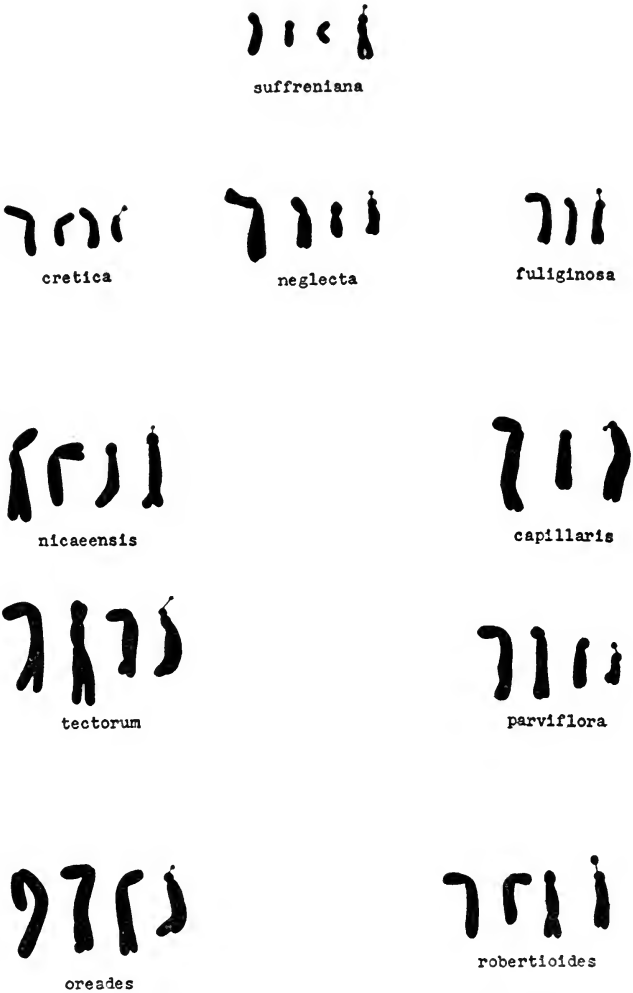

Fig. 8. Haploid complements of a group of *Eucrepis* species illustrating reduction in size of the chromosomes concurrent with reduction and specialization in the plant.

not of the most primitive category. *C. tectorum* is one of the most widespread annuals, whereas *C. nicaeensis* is a biennial (sometimes annual) of rather restricted distribution and probably a more recent species. *C. parviflora* and *C. capillaris* are closely related species with similar distributional areas in different geographic regions. Thus far, *C. capillaris* and *C. fuliginosa* are the only 3-paired species found in the genus, but they are not very closely related. It is believed that they were derived from different 4-paired ancestors. The four species at the top of the chart are very closely related. *C. neglecta* is of comparatively wide distribution, whereas *cretica* and *fuliginosa* are endemics and *Suffreniana* is very restricted. The last three are more reduced or highly specialized than *neglecta,* and undoubtedly they are comparatively recent in origin. These four species are of special interest because they illustrate the tendency of some of the recent *Eucrepis* species to merge into *Barkhausia.* This is indicated by their more or less definitely beaked achenes, especially in the three more recent species. Finally, this whole group of species is of unusual interest because of the probability that they have been derived from a 5-paired progenial line (see fig. 10).

By application of this method of comparing chromosome relations with the evidence from external morphology, the phyletic relations of all the *Crepis* species thus far studied cytologically have been worked out. These are represented in figures 9–11. The distribution of these various groups of related species may now be considered.

In *Catonia* (fig. 9) only three 10-chromosome species have thus far been obtained, but two of them, *sibirica* and *pontana,* are the most primitive types in the whole genus. The first is distributed from central Europe to Mongolia and southward to

Transcaucasia, and the second occurs at higher altitudes from France to Rumania. The third, *aurea,* is much less primitive and occurs in various forms in the mountains of southern Europe and northern Asia Minor. The 8-chromosome species fall into two groups, one with four, the other with six species. Of the first group, *blattarioides* and *alpestris* are montane species of southern Europe; the latter also occurs in Asia Minor, which supplements the evidence from gross and chromosome morphology that it had a common origin with *C. hypochaeridea* of

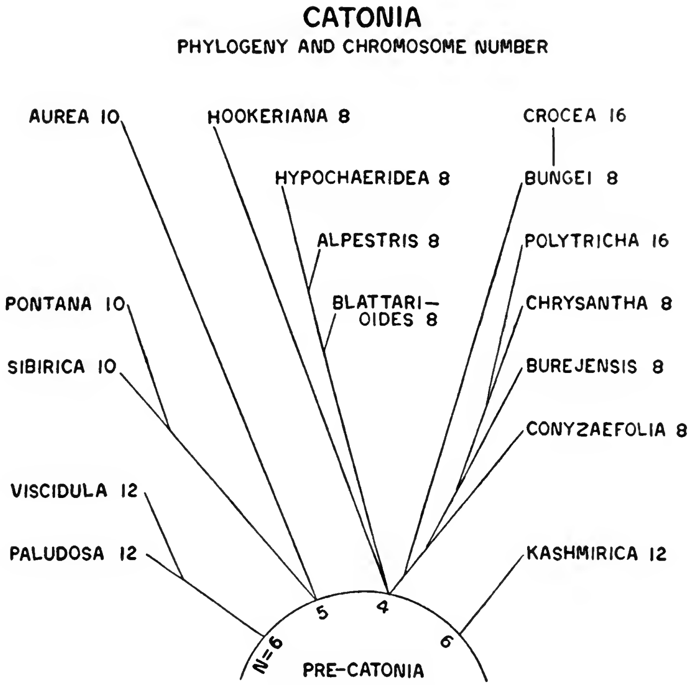

Fig. 9. Phylogeny and chromosome number in *Catonia.*

South Africa. Furthermore, there are central African species which are certainly related to *hypochaeridea,* and one of these, *C. Newii,* has just been found to have a genom very similar to that of *C. hypochaeridea.* The fourth species, *Hookeriana,* a Moroccan plant of the Grand Atlas Mountains, is less closely related to the other three. Of the second group, *conyzaefolia* is the most primitive species and is distributed from southern Europe to central Asia; the other five, all of eastern Asia, are certainly less primitive. Although the 12-chromosome *Catonia* species must be regarded as derived from species with some more primitive number or numbers, yet they are fairly primitive types. Their distributional relations are interesting, for *paludosa* is second only to *sibirica* in distributional range (western Europe to western Siberia), while its close relative, *viscidula,* is restricted to the northern Balkan countries. *C. kashmirica* is not closely related to the other two and it must have sprung from a different ancestor or ancestors; as its name indicates, it occurs in the western Himalaya Mountains. From this survey of *Catonia,* it would appear that the center of origin and distribution of these species must have been in south-central or southwestern Asia.

In *Eucrepis* (fig. 10) the 10-chromosome species comprise three groups, of which the first contains two alpine perennials, *C. Raulinii,* an endemic of Crete, and *C. bithynica,* which occurs in northern Asia Minor and the western Balkan Peninsula. The second group comprises *C. multicaulis,* a much less primitive perennial which is distributed from the western Himalayas to northern Scandinavia, together with *sancta* and *bifida,* two annuals which are closely related to each other and whose combined range is from southwestern Europe to southwestern Asia. The third group contains *tingitana,* a somewhat primitive perennial of northern Morocco and southwestern Spain which

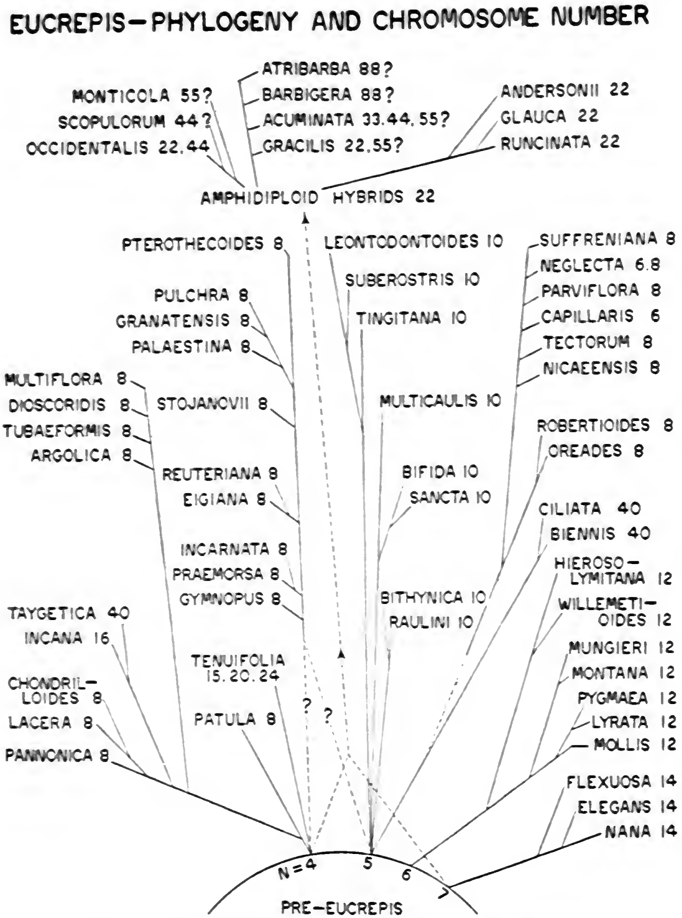

Fig. 10. Phylogeny and chromosome number in *Eucrepis*.

has some affinity with certain African species of *Catonia; suberostris,* an endemic annual of Algeria; and *leontodontoides,* a less primitive perennial of Italy and southern France.

The 8-chromosome *Eucrepis* species comprise several distinct groups, two of which have already been mentioned in connection with chromosome morphology. One of these, the *oreades-Suffreniana* series, may have originated from a 10-chromosome ancestral stock because there is a certain amount of affinity for the 40-chromosome species, *biennis* and *ciliata,* which are octoploids with 5 as base number. The evidence on distribution is in harmony with this idea. *C. biennis* is distributed from western Asia to western Europe and southward to southern Russia and the middle Balkans; *C. ciliata* occurs in the Caucasus region. *C. oreades* and *Robertioides* are woody-based alpine perennials, the former from middle Asia, the latter from Syria. *C. nicaeensis* occurs sporadically from the Balkan Peninsula to the Pyrenees; *tectorum* is distributed throughout most of Europe and the greater part of Siberia; *capillaris* is found in southern and middle Europe and eastward to southern Ukraine and Crimea; *parviflora* occurs from the eastern Balkans throughout Asia Minor to Egypt and the Caucasus; *neglecta* and its close allies are distributed from southern France to Asia Minor, Greece, and Crete. Likewise, the *gymnopus-pterothecoides* group, taken as a whole, ranges from Japan to Spain and from middle Russia to Palestine, with five of the ten species occurring in Syria.

The other two groups of 8-chromosome *Eucrepis* species are found in certain parts of the same general region. *C. pannonica, lacera,* and *chondrilloides* are very closely related species, and their distribution is in agreement with the morphological evidence of relative age. *C. pannonica* is certainly the most primitive and is distributed from Hungary to southern Russia, *lacera* is intermediate and occurs in the southern half of Italy, and *chondrilloides* is most recent and is found only in a limited area extending from Trieste into southern Austria and northern Dalmatia. (Associated with the foregoing are the two polyploid species, *C. incana* and *C. taygetica,* of southern Greece.) In the *argolica-multiflora* group, however, the relation between distribution and the morphological evidence of relative age is reversed. Both *argolica* and *tubaeformis* are the least specialized, particularly in achenial features, and each is known only from a single small area in Greece, whereas *dioscoridis* is abundant in parts of southern Greece, and *multiflora,* the most reduced species, occurs on the islands and shores of the Aegean Sea in eastern Greece and western Asia Minor. Hence these two groups of species illustrate very well the difficulty which was recognized by Willis[38] in applying the "age and area" hypothesis to very small groups of species—the *pannonica* group is in agreement with the hypothesis, but the *argolica* group is not. This, however, is merely an incidental observation. The main point is that both groups form part of the *Eucrepis* assemblage and occur in the same distributional area.

Definitely associated with the foregoing species, although not closely related to any of them nor to each other, are two remarkable species, *C. patula,* an endemic of northern Algeria, and *C. tenuifolia,* which is distributed from the western Himalayas to Mongolia. The former is apparently a relic which combines a number of primitive features with extreme reduction of the pappus, a combination of characters that is unique in the genus. The latter is believed to have originated as an interspecific hybrid between two 8-chromosome species followed by amphidiploidy and subsequent alterations in chromosome number.[2]

Turning now to other *Eucrepis* species with derived chromosome numbers, we find three groups, namely, those with 12 chromosomes, those with 14 chromosomes, and those having 22 chromosomes as the base number. As in the groups discussed above, the position of each species in the series (fig. 10) is determined on the basis of comparative morphology, considered with reference to geographic distribution which, in the 12-chromosome group, is as follows: *mollis* extends from western Europe to middle Asia; *lyrata* is found in western Siberia; *pygmaea* occurs only in the European Alps; *montana,* only in Greece; *mungieri,* only in Crete; *Willemetioides,* in northeastern Persia; and *hierosolymitana,* in Palestine, Syria and Cyprus.

At present only three species with 14 chromosomes are known, yet they comprise an even more widespread group than the preceding one. *C. nana,* in fact, is the most widespread species in the genus, being distributed from central Asia to eastern Labrador, at high elevations in the Rocky Mountains, and in the higher ranges of Utah, Nevada, and the Pacific Coast states. *C. elegans* occurs only in Alaska and the Rocky Mountains, and *C. flexuosa* is distributed from Outer Mongolia and Semipalatinsk to the Altai and Himalaya mountains.

The remaining *Eucrepis* species occur only in North America. As is indicated in the chart (fig. 10), there is good evidence to support the hypothesis that all these species with 22 as the base number originated through hybridization between 14-chromosome and 8-chromosome species followed by amphidiploidy. The region of origin is uncertain, but it seems most probable that it was in southern Alaska or an adjacent area to the south, and that the progenial species did not survive the subsequent glacial epoch in which their more vigorous offspring were able to migrate southward. At any rate, the distribution of these exclusively American species indicates a radiation from southwestern

Canada and northwestern United States to the east, southeast, and south. Furthermore, the existence of 14-chromosome species in North America previous to the last or Wisconsin glacial epoch, is proved by Fernald's discovery[12] of *C. nana* in an unglaciated island on the Gaspé Peninsula in eastern Canada. Although no 8-chromosome species are known to occur in Alaska, one such species (*C. burejensis,* which from its morphology might have been an ancestor of the *occidentalis* group of American species) is found in the Kurile Islands, and it might easily have been distributed farther east at an earlier period. It seems very probable, therefore, that these American species are descendants of 8- and 14-chromosome species which migrated into northeastern North America from Asia.

Reviewing the evidence on distribution of these various groups of related species in the subgenus *Eucrepis,* we find it consistently pointing to south-central Asia as the region of common origin.

In *Barkhausia* (fig. 11) the 10-chromosome species are certainly more primitive as a group than any of the 8-chromosome species. They may be considered in two subgroups, namely, those more or less resembling *C. albida,* and those clustering around *C. foetida. C. albida* is a polymorphous suffrutescent perennial species of southwestern Europe and the Grand Atlas Mountains in Morocco. *C. alpina* is a primitive type of annual which is distributed from the Caucasus to western Asia Minor, and *C. syriaca* is a closely related species occurring more to the south. *C. rubra* is a less primitive congener of the southern Balkans and Italy. It is worth noting, also, that there are two obviously related species in Abyssinia which have not yet been studied cytologically. There is thus sufficient evidence of connection between *albida* and the region of common origin for *Eucrepis* and *Catonia.* The species in the *foetida* group are more closely connected in distribution. *C. foetida* (including several subspecies) is distributed from southwestern Persia and the Caspian region through Asia Minor to western Europe; *commutata*

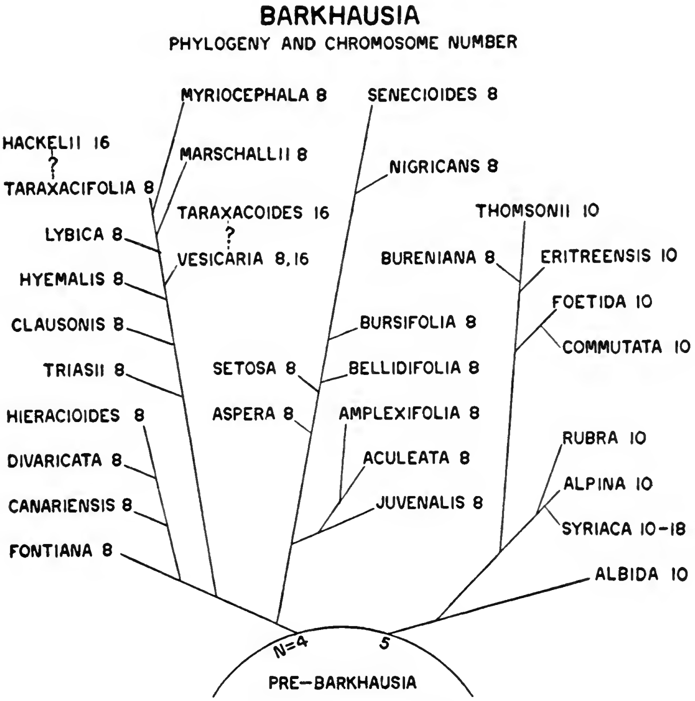

Fig. 11. Phylogeny and chromosome number in *Barkhausia.*

occurs in Asia Minor and the southern Balkans; *eritreensis* is known only from Eritrea; *Thomsonii* is indigenous in northwestern India; and the definitely affiliated 8-chromosome species, *C. Bureniana,* is a native of Persia, Baluchistan, and Afghanistan.

All the 8-chromosome *Barkhausia* species (fig. 11) are of the Mediterranean littoral, several being island endemics, including two from Madeira and one from the Canary Islands. Several are of rather wide distribution, while the tetraploid species connected with them are more restricted and undoubtedly more recent. It seems hardly necessary to go into further detail concerning their distribution, as they are certainly connected with Asia Minor and the Caucasus region.

In general, the evidence on distribution of related groups of *Crepis* species is wholly consistent with the assumption that the center of origin and distribution for the genus is in south-central Asia. It follows, then, that there was subsequent migration to the west, with the development of secondary regions of speciation in Asia Minor, the Balkan Peninsula, the European Alps, Abyssinia, and the Mediterranean littoral, and to the northeast, with secondary centers in the Altai region, northeastern Asia, and northwestern America. Although there are still many interesting problems to be solved with reference to specific relations and the nature of endemics,—concerning whether they are epibiotic or of recent origin,—the most fundamental problems may be considered as solved with the establishment of the center of origin in southwestern Asia and with the conclusion that 5 and 4 are the basic haploid chromosome numbers in *Crepis* and that 5 is the more primitive number.

ORIGIN OF THE CREPIDINAE

What bearing have these conclusions on the problem of origin in the *Crepidinae?* It is impracticable to give a detailed study of distribution in *Hieracium, Lactuca,* and *Prenanthes,* but it cannot be without significance that in each of these genera south-central Asia is centrally situated with reference to generic limits of distribution (fig. 1). Furthermore, the species of that unique smaller group, the *Glomeratae,* which show affinity for both

Crepis and *Prenanthes,* are confined to the Himalayan region. In addition, the most primitive species which has been excluded from *Crepis,* namely, *Paleya oligocephala,* occurs in this region only. The existence of these species in the Himalayas, however, need not be stressed, inasmuch as the origin of the *Crepidinae* may have antedated the upheaval of that great mountain system. This evidence on distribution, however, is consistent with the concept that *Crepis* and its closest allies originated in south-central Asia.

This leads naturally to the question of whether any genetical evolutionary processes can be suggested to account for speciation and differentiation within these genera. It has been intimated (p. 19) that our present knowledge of phylogeny in *Crepis* makes possible a tentative hypothesis of this kind. Before presenting this hypothesis, however, it is necessary to consider briefly two fundamental genetical processes which appear to have been operating in the evolution of *Crepis.* The first of these is reduction of chromosome number from 10 to 8. If monophylesis for the genus be assumed, it is necessary also to assume that such a process actually operated during the early development of the genus. Although there is no experimental evidence that new species can originate in this way, yet the combined evidence from comparative morphology, geographic distribution, and cytology in *Crepis* both necessitates and supports this assumption. It will be recalled that, although 10 is the most primitive number in the genus, yet 8 is found in the larger number of species and there are some rather primitive types among the 8-chromosome species. Furthermore, in certain groups of closely related species two different chromosome numbers occur. Thus the two 6-chromosome *Eucrepis* species are obviously related to species with 8 chromosomes, and in *Barkhausia* a 10-chromosome group contains one 8-chromosome species. It has been pointed out by Babcock and Cameron[2] that the most likely process by which 8-chromosome species might arise from 10-chromosome ancestors would be by reciprocal translocations between nonhomologous chromosomes, followed by meiotic irregularities leading to disappearance of one pair of chromosomes. The disappearance of a pair of chromosomes, however, does not necessarily imply actual loss of any essential genes. Reduplications of small sections of chromosomes are known to occur and these might compensate for the loss of fragments lacking a spindle-fiber attachment. There has come to light in recent years abundant evidence that reciprocal translocations between nonhomologous chromosomes occur in nature and that they may have a profound effect on genetic relationships. A mechanism is known to exist, therefore, which makes possible the origin of 8-chromosome species from 10-chromosome progenitors.

The other fundamental process involved is that of interspecific hybridization and amphidiploidy. That this phenomenon may be of great importance in the evolution of the higher plants has been amply demonstrated by the production, through artificial hybridization, of highly fertile and constant new forms which might be expected to maintain themselves under natural conditions.

The classical example to be investigated cytologically is that of *Nicotiana digulta* of Clausen and Goodspeed,[11, 10] who obtained it by crossing *N. tabacum* ($n = 24$) with *N. glutinosa* ($n = 12$). *N. digluta* has 36 pairs of chromosomes, is fairly fertile, and reproduces itself constantly. But when it was crossed with the parental species, the investigators found that the hybrid progeny were more or less fertile and displayed a tendency to revert to the types of the parental species. Thus, although *N. digluta* behaves like a distinct species, it probably could not survive under natural conditions unless isolated from the parental species. This was the first experimental verification of the hypothesis proposed by Winge,[30] that interspecific hybridization followed by doubling of the chromosome number might account for the arithmetical series of chromosome numbers which have been shown to exist in various genera of plants. Since then, numerous amphidiploid hybrids between distinct species have been produced experimentally and many of them behave like "good" species although many others are more or less sterile and irregular in reproduction. One of the most convincing examples is that of *Raphanobrassica,* which was produced by Karpechenko[20] by crossing *Raphanus sativus* with *Brassica oleracea.* The amphidiploid race obtained is constant and fertile under experimental conditions, and can be crossed with the parental species only with great difficulty; hence it must be considered a potential new species. Furthermore, numerous constant interspecific hybrids have been discovered in nature, and these presumably arose through amphidiploidy.[29, 30, 40]

In *Crepis,* cytological evidence has been found to indicate the important rôle played by interspecific hybridization and amphidiploidy in the evolution of this genus (pp. 29, 38, 41). It may be objected that the experimental evidence from *Crepis* does not support this idea. It happens, however, that the three amphidiploids thus far obtained in *Crepis* resulted from crosses between nearly related species, so that there was sufficient homology between the chromosomes of the parents to cause much irregularity in distribution of the chromosomes to the gametes, with resulting sterility.[29] The fact that amphidiploids were produced from hybrids between such species may be looked upon as supporting the hypothesis here proposed.

If it be admitted that two such genetical processes as reduction in chromosome number from 10 to 8, and interspecific hybridization followed by amphidiploidy, may have occurred in the early evolution of this group of plants, a working hypothesis of the origin of the *Crepidinae* is readily forthcoming. This hypothesis is illustrated diagrammatically in figure 12, and may be stated as follows:

(1) The original progenial stock consisted of one or more 10-chromosome species.

(2) New species with 8 chromosomes originated through some such process as reciprocal translocation with subsequent elimination of parts of chromosomes, leading eventually to the disappearance of one pair of chromosomes.

(3) The genus *Crepis* arose from the complex of species thus created.

(4) The 8- and 9-paired species of closely related genera originated through interspecific hybridization between 5-paired and 4-paired species (or between 4-paired species) followed by amphidiploidy.

(5) Speciation and evolution, within *Crepis* at least, have involved the same fundamental processes together with autopolyploidy, and, concurrently with these processes, genic mutation has played a continual rôle.

The propositions just stated are submitted as the most logical conception of the early course of evolution in the *Crepidinae* on the basis of the evidence now available. Future research on *Crepis* and especially on the genera closest to *Crepis* may result in modification or extension of the hypothesis, but it appears that the general nature of the processes involved in the evolution of this group of plants has been disclosed. If this working hypothesis ultimately becomes an established theory, it will necessitate the recognition that gross chromosomal alterations have played a more basic rôle, in the evolution of some of the higher plants, at least, than has genic mutation.

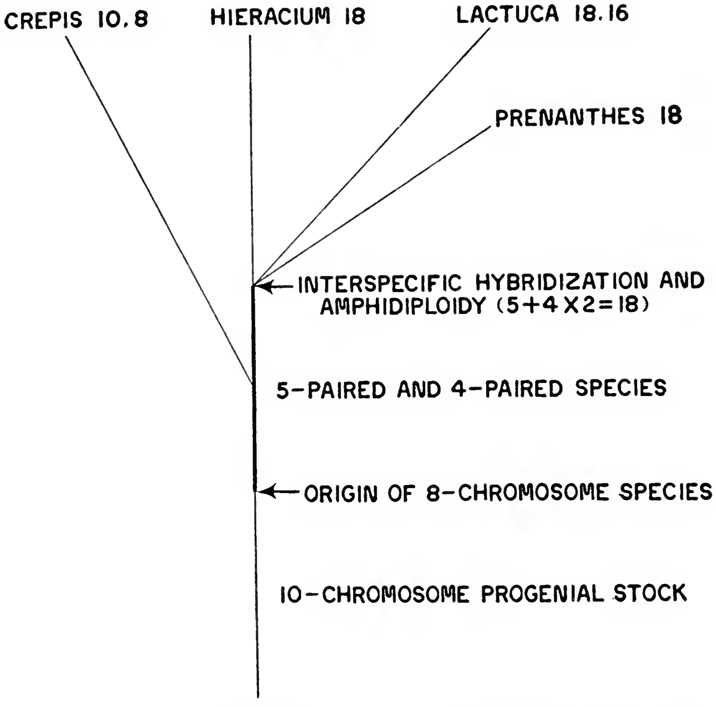

Fig. 12. Origin of the *Crepidinae*. The diagram illustrates the hypothesis that the whole subtribe originated from a 10-chromosome stock through: (1) origin of 8-chromosome species by loss of one pair of chromosomes; (2) development of *Crepis* from this group of 5-paired and 4-paired species; (3) origin of the other genera through interspecific hybridization between some of those species followed by amphidiploidy.

A detailed discussion of various pertinent questions which will arise in the minds of critical readers must be postponed until a future contribution. Let it suffice for the present to state that, in the mind of the present writer, all such queries revolve around problems which are of minor importance as compared with the genetic evolutionary processes on which the hypothesis is based. One such question may be mentioned briefly by way of illustration.

An interesting issue is raised because, in those few species in the genera related to *Crepis* on which data are available, there appears to be only one pair of satellite-bearing chromosomes. This may at first appear inconsistent with the fact that certain species of *Crepis* are believed to have arisen through interspecific hybridization and amphidiploidy because they have two or more pairs of unlike D chromosomes. This criticism can be met by reference to the phenomenon known as amphiplasty.[25] It has been found that, in hybrids between certain species, the satellite contributed by one of the parental species is permanently lost, whereas in other interspecific hybrids the satellites from both parents are preserved. These well-established facts are sufficient to account for the apparent inconsistency.

The genus *Crepis* is closely related to the other genera of the *Crepidinae,* if the evidence from comparative morphology can be trusted, and probably it can be, especially when it leads to the same conclusion as other criteria. The genus *Crepis,* in spite of the great variability in chromosome numbers which it exhibits, is a natural group with a common center of origin and a single, most primitive chromosome number. The center of origin of *Crepis* coincides with the center of origin for its closest allies. Only on cytological grounds is there an apparent separation of *Crepis* from other genera in this group. A hypothesis has been proposed which seems to account satisfactorily for these chromosome relations and to be consistent with other evidence of natural relationship in the *Crepidinae.*

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The Succession and Distribution of Cenozoic Floras Around the Northern Pacific Basin

By Ralph W. Chaney

The vegetation of western North America in the Cenozoic era has been made known by the studies of Lesquéreux, Newberry, and Dawson, followed by a more modern group, among whom Knowlton was the outstanding contributor. Until recently, however, the floras of this most recent major unit of geologic time, occupying perhaps the latest hundred million years of the earth's history, have not been critically studied on the continent of Asia. With the investigations of Kryshtofovich and others, it becomes possible to compare Tertiary floras on both sides of the Pacific Basin, and to determine not only their sequence in geologic time, but also their probable routes of migration and their modern geographic situation. The purpose of this paper is to summarize the evidence of the succession and distribution of the Cenozoic floras around the northern part of the Pacific Basin, and to outline the general principles which guide the interpretation of this evidence.

The underlying basis for the interpretation of the distribution of Cenozoic floras, both in time and in space, is the assumption of a trend from mild, humid climate at the early part of the era to cool, semiarid climate toward its close. This does not imply that there were not minor changes in reverse direction in the Cenozoic, nor that the change toward cooling and drying was of uniform rate. A series of fossil floras resulting from such a climatic trend is an example of what Clements[1*] has termed a

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[*] Superior figures refer to items in the bibliography at the end of this essay.

clisere, that is, a sequence of climaxes with the corresponding climates, such as may be seen today from the foot to the summit of high peaks or from tropical to polar lands. Not only does the fossil plant record of the Cenozoic indicate such a cliseral sequence, but also the evidence of the animals, both invertebrate and vertebrate, and of the sedimentary rocks in which they are enclosed, is in accord with the assumption of this climatic trend through the Cenozoic. It has been discussed on the basis of the plant record in several publications by the writer and his associates,[2, 3, 4, 5, 6, 7, 8] and will not be reviewed here in detail.

Floras of older Tertiary age, including those referred to the Eocene epoch and some of those referred to the Oligocene,* have been critically studied in western North America from the west flank of the Sierra Nevada in central California, from the western border of the Cascade Range in central Oregon, from the John Day Basin of eastern Oregon, from the Puget Sound area and from the eastern slope of the Cascades in Washington, and from the Kenai Peninsula and adjacent Alaska.† These floras as represented in California and Oregon are made up dominantly of types of plants which have their modern range in the low latitudes of both hemispheres. Silicified stems make up a conspicuous part of the fossil record in the Auriferous

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* Confusion concerning the boundary between these two series of the Tertiary in western North America often makes impossible an exact age designation. The terms "Eocene" and "older Tertiary" as applied to American floras will be used synonymously in this paper, since most of the floras discussed are considered by the writer to be of Eocene age.

† In addition to the papers listed in the bibliography, the following studies have advanced to the point of completed manuscript or of matured conclusions: C. A. Hollick, on the Tertiary floras of Alaska; R. S. LaMotte and others, on the floras of Washington; R. W. Chaney, on the Clarno flora of eastern Oregon; H. D. MacGinitie, on the older Auriferous Gravels floras of California.

Gravels of the Sierra foothills, but they are rare or absent at the other localities, as are seeds and flowers. Leaves are the structures most commonly preserved, occurring in the tuffaceous shales as impressions which show all the details of margin, nervation, and texture. The propriety of referring these leaf impressions to modern genera has been questioned on many occasions by botanists who feel that generic characters are neither constant nor recognizable in foliar structures. The paleobotanist, however, usually dependent on the evidence of leaves, has been forced to find in them criteria for recognition which are unknown to most botanists; he sees in the arrangement of the nerves, particularly near the margin, diagnostic characters by which a relationship to modern genera can often be established; with certain specimens he may be forced to indicate only a family relationship by the use of such names as *Laurophyllum, Leguminosites,* or *Menispermites.* Familiarity with the foliage of modern plants in forest and herbarium makes possible his reference of almost all leaf fossils to genera which indicate their systematic position, leaving only a small residue in the form genus *Phyllites.* It is significant to note that botanists of wide experience in field and herbarium, such as Abrams, Jepson, and Mason for temperate floras, and Gleason, Greenman, Merrill, Standley, and Wilson for those of lower latitudes, are able to recognize readily the leaves of modern woody plants, and to suggest the generic or family affinities of fossil leaves as well. Acknowledgment is due to these and many other botanists for the valuable assistance which they have given to the writer and his associates.

As compared with the species of later Tertiary floras, Eocene leaves are large and thick, with the margins more commonly entire and with a consequently greater development of camptodrome nervation. The families which are most characteristic, together with the genera included in them, are given in the following list:

- Palmaceae
  - Sabalites
- Liliaceae
  - Smilax
- Juglandaceae
  - Engelhardtia
- Fagaceae
  - Quercus
- Moraceae
  - Ficus
  - Pourouma
- Aristolochiaceae
  - Aristolochia
- Trochodendraceae
  - Trochodendroides (Tetracentron)
- Menispermaceae
  - Abuta
  - Cissampelos
  - Menispermites
- Magnoliaceae
  - Drimys
  - Magnolia
- Anonaceae
  - Anona
- Monimiaceae
  - Siparuna
- Lauraceae
  - Acrodiclidium
  - Cinnamomum
  - Cryptocarya
  - Lindera
  - Nectandra
  - Ocotea
  - Persea
- Hamamelidaceae
  - Liquidambar
- Platanaceae
  - Platanus
- Leguminosae
  - Inga
  - Lonchocarpus
  - Mimosites
- Euphorbiaceae
  - Acalypha
  - Alchornea
  - Aleurites
  - Aporosa
  - Euphorbiophyllum
  - Mallotus
  - Sapium
- Anacardiaceae
  - Astronium
- Sapindaceae
  - Allophylus
  - Cupania
- Sabiaceae
  - Meliosma
- Rhamnaceae
  - Rhamnidium
- Sterculiaceae
  - Pterospermum
  - Sterculia
- Dilleniaceae
  - Davilla
  - Tetracera
- Flacourtiaceae
  - Xylosma
- Myrtaceae
  - Calyptranthes

- Araliaceae
  - Aralia
- Sapotaceae
  - Chrysophyllum
  - Lucuma
- Ebenaceae
  - Diospyros
- Styracaceae
  - Styrax
- Apocynaceae
  - Apocynophyllum
- Boraginaceae
  - Cordia
  - Ehretia
- Verbenaceae
  - Petrea
- Bignoniaceae
  - Callichlamys
- Caprifoliaceae
  - Viburnum

Ferns and gymnosperms have not been included because of their comparative rarity in older Tertiary floras of western America.

The plants listed indicate a climate characterized by an annual rainfall of not less than 80 inches and by a uniform temperature free from frost—a climate (to mention only those regions with which the writer is familiar) essentially like that on the lower slopes of Vera Cruz, Mexico, up to an elevation of 5500 feet on the Pacific slope of Guatemala, in the savannas near sea level on the Pacific slope of Panama, and at an elevation of about 5000 feet in the Andes of Venezuela near Mérida. There is evidence that the Goshen flora advanced northward from low latitudes to its Eocene or Oligocene position in west-central Oregon.[9] A similar movement has been described for the somewhat older Wilcox flora of the southeastern United States.[10] Knowledge of the Cretaceous floras of western America is so scant as to give little information about the pre-Eocene distribution of the families and genera involved, although it has been pointed out that some of the genera and most of the families were widely distributed.[11] If this movement from low latitudes can be demonstrated, it will represent the most extensive northward migration recorded by plants in the Cenozoic era, and the only migration of importance in that direction until the Pleistocene or Recent, when the coniferous forest was shifted from southern to central and northern California.[12, 13]

The study of the Eocene floras of Washington has not yet advanced to a point where a list of the families and genera represented can be given. Although numerous species represented in the states to the south are included, indicating that the northward movement above mentioned extended into this state, the leaves are for the most part characterized by smaller size, thinner texture, and more commonly serrate margins. It seems clear that they represent a less tropical assemblage than do those of Oregon and California and that their modern equivalents will be found in temperate rain forests of higher latitudes. The same conclusion may be reached concerning the Eocene floras from the Rocky Mountain province to the east. As now described, these floras include a large list of temperate genera such as *Acer, Alnus, Betula, Cornus, Fraxinus, Populus,* and *Ulmus,* along with subtropical types. Although many of the generic references must be revised before the lists of names can be depended upon as an indication of the nature of these floras, a survey of the average size, margins, and texture of the leaves as figured indicates that they represent a more temperate assemblage than those along the Pacific Coast at the same latitudes. This may be explained as resulting from the more continental type of climate in the Rocky Mountain province as compared to that of the Pacific border states.

The Kenai flora of Alaska, considered by Hollick and others to be of Eocene age, includes such genera as *Diospyros, Ficus,* and *Magnolia;* but the most conspicuous and widespread element of this flora comprises such genera as *Acer, Alnus, Betula,* *Carpinus, Castanea, Cercidiphyllum, Corylus, Fagus, Ginkgo, Juglans, Liquidambar, Myrica (Comptonia), Platanus, Populus, Prunus, Quercus, Salix, Sequoia, Taxodium, Tilia, Trapa,* and *Ulmus.* The abundance of *Sequoia* emphasizes the temperate aspect of this flora, which with slight modifications has been recorded from several other Eocene localities in the Arctic including Greenland and Spitzbergen. A flora of older Tertiary age, collected by Mason and others[14] on the shore of the Bering Sea south of Nome and on St. Lawrence Island, is made up of *Alnus, Platanus, Sequoia,* and other temperate genera.

The significance of older Tertiary floras of Siberia, together with those of Manchuria, Korea, and adjacent parts of northeastern Asia, has been admirably summarized by Kryshtofovich.[15] He concludes that nowhere in this region during the Tertiary were there tropical or subtropical conditions, but that as late as the Lower Miocene it was occupied by a deciduous forest "composed mostly of temperate types such as *Fagus, Ulmus, Alnus, Betula, Corylus, Populus, Juglans, Comptonia,* and *Trapa*." He points out the similarity of this flora to that from the Eocene of Alaska, and the marked difference between it and the subtropical floras of older Tertiary age in western Europe. His explanation of the cause of this difference is perhaps open to question, involving as it does the supposed migration of the North Pole to the northern part of the Pacific. It seems apparent that the southwestern part of Eurasia, extensively submerged in early Tertiary time, must have been characterized by a much warmer climate than the northeastern part of this land mass, far removed from the ameliorating influences of the Atlantic. In any event, with the pole in its present position, the climatic differences between these two parts of Eurasia are almost as great today as those indicated for the Eocene. In addition to latitude the major factor in determining these differences seems to be the position of the two areas with relation to prevailing circulation of air and water currents. The resemblance of these early Tertiary floras of Alaska and northeastern Asia to the Miocene floras of Oregon and adjacent states will be seen by reference to the list of Miocene genera on page 68. It seems possible to conclude that in the early part of the Tertiary period there was no such uniformity of climate over a wide range of latitude as has been pictured by earlier writers, some of whom are responsible for the myth of the occurrence of tropical floras in the Arctics. The existence of such floras has been so frequently disproved by Berry[16] and others in recent years that their supposed climatic implications can be wholly disregarded. The fossil plant record indicates that there were differences in temperature and humidity along the Pacific Coast of North America during the Eocene which, though perhaps not as marked as those of today, indicate that latitude was a controlling factor, with subtropical vegetation toward the south and progressively more temperate floras northward into Alaska. The differentiation of Tertiary vegetation into a series of climaxes, or a clisere, in response to differences in latitude and altitude was suggested by Clements almost twenty years ago.[17]

This change in the character of the vegetation because of the influence of latitude makes possible certain important inferences concerning the nature of the upland forests during the Eocene and subsequent epochs. The fossil record is of necessity incomplete, since it is usually preserved at sites of deposition situated on the lowlands. Studies of the dispersal of modern leaves and fruits from the trees on which they grew indicate that under normal conditions of transportation they are rarely deposited except in the immediate vicinity of the parent trees. The assumption may readily be made that all the more common plant remains in a fossil deposit are of lowland types, from trees adjacent to the site of deposition. The actual record is, therefore, of these plants which grew in lowlands, where the accumulation of their leaves and other structures is made possible by their inclusion in sedimentary deposits. In the Tertiary of North America there are only occasional remains, such as wind-borne seeds and leaves of exceptional durability, which give material evidence of the nature of upland vegetation.

It seems obvious that in any Tertiary situation the trees of the upper slopes and ridges had a more xerophytic aspect than that of the flood plain, lake borders, and coastal lagoons, the vegetation of which has been preserved in the fossil record. Just as the redwood forest of today has a border phase dominated by Douglas fir, live oak, and madrone, and as the rain forest of the tropics grades up into an association characterized by oaks and other temperate trees, so the redwood forest of the Miocene and the rain forest of the Eocene may be assumed to have had border phases conditioned by less humid climate the temperate range of which was more extreme. The nature of these border phases can rarely be directly determined from an adjacent fossil record, since only exceptionally has the upland vegetation been preserved in sedimentary deposits. An indirect but effective method of determining the nature of the vegetation of the uplands may be followed by examining the contemporary floras of higher latitudes. In the same manner as the high altitude border phase of modern climax forests shows a parallel development in higher latitudes near sea level, the upland vegetation bordering a Tertiary climax in middle latitudes may be indicated by the nature of the fossil record to the north, at lowland situations suited to its deposition and preservation.

The presence of a typically temperate forest in Alaska during the Eocene therefore makes possible the assumption that a similar assemblage occupied the uplands in Oregon and California at the time that the Goshen, Comstock, and other subtropical forests were living in the lowlands and shedding their leaves into adjacent basins of deposition. Unquestionably, there were differences in detail between these contemporary forests of high altitudes and high latitude; in the upland forest, *Pseudotsuga* or *Abies* may have taken the place of northern *Sequoia* as a dominant in the same way that *Pinus* and *Abies* supplant the dominant *Picea* of high latitudes in the subalpine forests of middle latitudes today. But the general aspect of the Eocene forest of the uplands may be reconstructed on the basis of the contemporary floras at high latitudes. Of further significance is the fact, already mentioned, that this Eocene vegetation of high latitudes, presumably deposited near sea level, and the Eocene vegetation assumed to have been present in the uplands of middle latitudes, have a definitely Miocene aspect. The upland vegetation of Oregon and California during the Eocene epoch did not become part of the fossil record because it was destroyed in the course of transportation toward areas of deposition in the lowlands. With the lowered humidity and temperature of Miocene times, it was shifted downward toward sea level from the uplands, until it came to occupy the sites of deposition in which the earlier floras had accumulated in the Eocene. At the same time the southern limit of the high-latitude forest was shifted down from Alaska into Oregon and California. Thereafter this temperate flora entered the fossil record as the well-known redwood forest of the Miocene. Certain differences may be recognized between the middle-latitude Miocene flora and its high-latitude Eocene equivalent. But these are no greater than might be expected in view of the length of time involved and the distance covered. It is significant to note that this forest, characteristic of the lowlands of Oregon and adjacent states during the Miocene, was present in only slightly modified form at higher latitudes on both sides of the Pacific during early Tertiary time, and that its high-altitude equivalent may be assumed to have occupied the upper slopes and ridges as far south as California. To a tradition-bound stratigraphic paleontologist, the occurrence of a "Miocene" flora in the uplands of Oregon and California during the Eocene epoch may prove disquieting, and may result in the conclusion, not infrequently expressed, that plant fossils are of little value as time indicators.* With no denial that homotaxiality, of both fossil floras and faunas, may be used as a rough basis for synchroneity in the dating of sedimentary formations, the conclusion may be expressed that for any detailed knowledge of the age of a fossil occurrence, data concerning latitude, altitude, and position with relation to ocean basins are essential. For the equally important considerations relating to the distribution and physical indications of the life of the past, such data are obviously required.

In this connection it seems desirable to quote a statement written in 1879 by J. S. Gardner.[18] This statement was not read by the present writer until after the preceding discussion in this paper had been completed. It indicates the early recognition by paleobotanists of the need for knowing something about the geographic occurrence of a fossil flora before its age can be determined:

The nearly unbroken sequence seen in the Eocene floras extends

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* It should be borne in mind, however, that because of its remoteness from sites of deposition, this upland flora with Miocene characteristics did not enter the record during the Eocene epoch. The critical feature in stratigraphic dating is not the time of existence of a flora or fauna, but the time of its entrance into the sedimentary record.

into the Miocene. There is no great break in passing from one to the other when we compare them over many latitudes, and but little change beyond that brought about by altered temperature or migration. But if Tertiary floras of different ages are met with in one area, great changes on the contrary are seen, and these are mainly due to progressive modifications in climate, and to altered distribution of land. From Middle Eocene to Miocene the heat imperceptibly diminished. Imperceptibly, too, the tropical members of the flora disappeared; that is to say, they migrated, for most of their types, I think, actually survive at the present day, many but very slightly altered. Then the sub-tropical members decreased, and the temperate forms, never quite absent even in the Middle Eocene, preponderated. As decreasing temperature drove the tropical forms south, the more northern must have pressed closely upon them. The Northern Eocene, or the temperate floras of that period, must have pushed, from their home in the far north, more and more south as climates chilled, and at least, in the Miocene time, occupied our latitudes. The relative preponderance of these elements, I believe, will assist in determining the age of Tertiary deposits in Europe, more than any minute comparisons of species. Thus it is useless to seek in the Arctic Regions for Eocene floras, as we know them in our latitudes, for during the Tertiary period the climatic conditions of the earth did not permit their growth there. Arctic fossil floras of temperate, and therefore Miocene aspect, are in all probability of Eocene age, and what has been recognized in them as a newer or Miocene facies is due to their having been first studied in Europe in latitudes which only became fitted for them in Miocene times.

When stratigraphical evidence is absent or inconclusive, this unexpected persistence of plant types or species throughout the Tertiaries should be remembered, and the degrees of latitude in which they are found should be well considered before conclusions are published respecting their relative age.

In response to physical changes controlled apparently by emergence with its resultant modification of ocean currents, and by mountain-making with its resultant modification of atmospheric circulation, a temperate forest came to occupy the lower altitudes in western North America in the Miocene epoch. Since it lived in situations suited to the preservation of leaves and other parts of the plants, this forest has left a plentiful and widespread record from California north to southern British Columbia, and eastward across Idaho and Nevada into Montana and Colorado. By the end of the Miocene, reduction in rainfall and temperature, with associated orogeny, had greatly restricted its distribution and limited its opportunities for entering the fossil record. This forest has survived, with important modifications, in many limited areas in western North America. The presence of its altered modern equivalent in the eastern United States at the present time suggests that in the Miocene it may have occupied this area as well, but the fossil record of its occurrence there is too scant to establish definitely such a distribution.

The dominant species of the Miocene floras of western America is *Sequoia langsdorfii,* the Tertiary equivalent of the living *S. sempervirens,* the coast redwood. Present in the older Tertiary floras of Alaska and northeastern Asia, this species is completely absent from the Eocene deposits of California and Oregon.* It is much reduced in distribution in the Pliocene epoch, and may therefore be used as an accurate index fossil for the Miocene of middle latitudes. The climatic and other physical requirements of the modern coast redwood are so restricted as to make its Tertiary equivalent a valuable indicator of past environments. Particularly is this true where remains of *Sequoia langsdorfii* are found with those of *Alnus, Quercus (Lithocarpus), Umbellularia,* and other genera which are its most regular associates along the northern coast of California at the present time. Ex-

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* *S. langsdorfii* is recorded from the upper Eocene of northwestern Washington, in a flora intermediate between the typical subtropical type from the Eocene of more southern latitudes and the typical temperate type from the Eocene of Alaska.

tensive quantitative studies involving a comparison of the frequency of occurrence of leaves and fruits in Tertiary deposits and in contemporary stream deposits have been carried on by the writer in the past fifteen years. From numerous localities, of both Miocene and Recent deposition, a large amount of data has been compiled which shows that *Alnus, Quercus (Lithocarpus), Sequoia,* and *Umbellularia* made up the same dominant element in the redwood forest of the Miocene as these genera do today. A count of 20,611 fossil specimens from the type locality of the Lower Miocene Bridge Creek flora, in the John Day Basin of eastern Oregon, has shown that four fossil species of the above-named genera make up 86.44 per cent of the total; a count of 8422 modern specimens from a valley in Muir Woods, near the coast of central California, has shown that the four modern equivalents of these genera make up 85.44 per cent of the total.[19] The general aspect of the Miocene forest, particularly in the early part of the epoch, must have been strikingly similar to that of the redwood belt on the California coast. A survey of the following list of the common families and genera of the Miocene floras of western North America will emphasize, however, the presence of two important elements which are no longer dominant or present there.

- Ginkgoaceae
  - Ginkgo
- Taxaceae
  - Taxus
  - Torreya
- Pinaceae
  - Abies
  - Picea
  - Pinus
  - Pseudotsuga
  - Tsuga
- Taxodiaceae
  - Glyptostrobus
  - Sequoia
  - Taxodium
- Cupressaceae
  - Libocedrus
  - Thuyites
- Liliaceae
  - Smilax

- Salicaceae
  - Populus
  - Salix
- Myricaceae
  - Myrica (Comptonia)
- Juglandaceae
  - Juglans
  - Hicoria
- Betulaceae
  - Alnus
  - Betula
  - Carpinus
  - Corylus
  - Ostrya
- Fagaceae
  - Castanea
  - Castanopsis
  - Fagus
  - Quercus (including Lithocarpus)
- Ulmaceae
  - Celtis
  - Ulmus
- Trochodendraceae
  - Cercidiphyllum
- Berberidaceae
  - Odostemon
- Lauraceae
  - Sassafras
  - Umbellularia
- Saxifragaceae
  - Hydrangea
  - Philadelphus
- Hamamelidaceae
  - Liquidambar
- Platanaceae
  - Platanus
- Rosaceae
  - Amelanchier
  - Cercocarpus
  - Crataegus
  - Prunus
  - Ribes
  - Rosa
  - Sorbus
- Leguminosae
  - Cercis
  - Leguminosites
- Anacardiaceae
  - Rhus
- Aceraceae
  - Acer
- Hippocastanaceae
  - Aesculus
- Sapindaceae
  - Sapindus
- Rhamnaceae
  - Ceanothus
  - Rhamnus
- Tiliaceae
  - Tilia
- Onagraceae
  - Trapa
- Cornaceae
  - Cornus
  - Nyssa
- Ericaceae
  - Arbutus
- Oleaceae
  - Fraxinus
- Caprifoliaceae
  - Viburnum

The more important of the two elements of the Miocene flora which are absent or sparsely represented in the living forests of western North America is the deciduous element comprising such genera as *Carpinus, Castanea, Fagus, Hicoria, Liquidambar, Nyssa, Ostrya, Sassafras, Tilia,* and *Ulmus.* Whereas such genera as *Acer, Aesculus, Alnus, Amelanchier, Betula, Cornus, Corylus, Fraxinus, Juglans, Philadelphus, Platanus, Populus, Prunus,* and *Salix* have survived on the Pacific Coast, retaining their deciduous habit, *Ceanothus, Quercus, Rhamnus,* and *Rhus* are predominantly evergreen; and a group of genera including many of the most numerous and wide-ranging forms in the modern forest—*Arbutus, Castanopsis, Lithocarpus (Quercus), Myrica, Odostemon,* and *Umbellularia*—are evergreen. A tentative suggestion may be made that the source of this element was in the south. The extensive representation of modern species of *Lithocarpus* in the low-latitude forests of Asia, and of evergreen members of the Lauraceae in the tropics of both hemispheres, suggests that their ancestors, shifting northward in the Eocene, may have survived in California and Oregon, or have continued their migration in the Miocene. There is some indication from the paleontologic history of the Ericaceae that they also had their origin in the south. In any event, the present abundance of broad-leafed evergreens in low latitudes and their known occurrence there in Cretaceous and Eocene time makes plausible the suggestion of their southern origin. The elimination of a large number of deciduous genera from the flora of western America, with an increased number of broad-leafed evergreens, appears to be related to fundamental changes in climate since the Miocene, involving the concentration of rainfall in the winter months. This Lower Miocene flora as a whole indicates a temperate climate over much of western

North America which was characterized by annual precipitation of at least 40 inches, probably more evenly distributed throughout the year than at present. The mild, uniform temperature in which frost played an inconspicuous part was controlled by the adjacent Pacific, whose influence extended farther inland than it does today, extensive highlands not being present until a later epoch of the Tertiary.

The second Miocene element, now missing from the forests of North America, comprises a group of genera and species which have survived in Asia. Such genera as *Cercidiphyllum, Ginkgo, Glyptostrobus,* and *Trapa* no longer occur outside of Asia. Other genera, still represented in North America, have species living in Asia which are more similar to the Miocene members of these genera; examples, with the fossil species in parentheses, are *Acer pictum* (*A. scottiae*), *Castanea henryi* (*C. orientalis*), *Crataegus pinnatifida* (*C. newberryi*), *Quercus myrsinaefolia* (*Q. consimilis,* in part), *Rhus sylvestris* (*R. merrillii*), and *Ulmus parvifolia* (*U. brownellii*).

In this connection, it is of interest to note that the genus *Sequoia,* now extinct in Eurasia, was widely distributed over that continent in the Tertiary. If the specific characters of various dicotyledonous species from the Miocene of Asia were better known to the writer, it seems probable that he would be able to include in addition a list of modern species from North America which are as closely related to them as are the living Asiatic species of their genera, or even more nearly than these. In any event, although the Miocene floras of Asia are at present incompletely studied, it is apparent that they include numerous genera such as *Acer, Alnus, Carpinus, Fagus, Populus, Sequoia,* and *Tilia,* which are characteristic of this epoch in North America. There appears to be much less difference between the Miocene and Eocene floras of Asia than between those of the same series in western North America. This may be accounted for by the comparative remoteness of the Asiatic floras from the Atlantic Ocean and its climatic effects; whereas changes in temperature of the Pacific were readily translated to the Tertiary floras of western America, similar changes in the Atlantic from the Eocene to Miocene epochs had less effect upon the Miocene floras of central and eastern Asia because of its distance from the region they occupied. In like manner many Miocene genera, particularly of deciduous types, have survived to the Recent in the temperate parts of eastern Asia. The living forests of northern Japan, Korea, Manchuria, and northern China, as observed by the writer, have a definitely Miocene aspect. The resemblance of these forests to those of eastern North America was long ago recognized by Asa Gray,[20] who suggested a past interchange of vegetation between the two areas across high latitudes. In the light of modern studies of later Tertiary floras and their distribution, it seems possible to conclude that this deciduous element, comprising genera and species from both sides of the Pacific, has survived on the eastern sides of both continents under climatic conditions involving summer rain and winter cold. The gradual elimination of deciduous types from the forest of the Pacific Coast, with the resultant dominance of broad-leafed evergreens, has resulted from the development there of a climate characterized by mild, rainy winters and cool, dry summers.

Comparison of the list of older Tertiary families and genera of Oregon and California (pp. 58–59), and of the list of Miocene families and genera (pp. 68–69), emphasizes that there is a great difference in their composition. With unimportant exceptions, the families and genera of the Eocene have their most extensive modern development in the warmer parts of the world, while those of the Miocene are in large part restricted to temperate areas. Where the same families fall in both lists, as do the Liliaceae, Juglandaceae, Fagaceae, Lauraceae, Leguminoseae, and Anacardiaceae, they are for the most part represented in the two floras by different genera, which are tropical in the Eocene and temperate in the Miocene. In the lists as here composed, the only genera common to both are *Liquidambar, Platanus, Quercus, Smilax,* and *Viburnum,* all of which are ancient genera of wide distribution since the Cretaceous, ranging at the present time from temperate lowlands to middle altitudes in the tropics. It must be admitted that if all the genera reported from the Miocene, especially by the older authors, were included in the list (pp. 68–69), the resemblance between this list and the Eocene flora would be more marked. Such genera as *Anona, Aralia, Cinnamomum, Diospyros, Ficus, Persea,* and *Sterculia* have been regularly recognized in Miocene floras, but usually on evidence which is not accepted by the writer. While it is possible that an occasional representative of a tropical genus may have survived as a relict in the Miocene floras of western America, this in no way affects the general conclusion that the members of the older Tertiary forests had in large measure disappeared from the middle latitudes before the beginning of the Miocene. With altered climatic conditions, the northern limits of the ranges of the typical Eocene species shifted southward, and the temperate types of higher altitudes and latitudes moved down to take their places as the forest dominants of Oregon and California. Many of these* have continued to live in western America down to the present time, but subsequent changes in topography and climate have restricted their distribution to the most favored situations.

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* To almost every Tertiary species, a name different from that of its modern equivalent has been applied, but the actual differences as based on leaf characters may not always warrant these specific designations.

The forest dominated by the coast redwood is confined to a narrow belt along the coast from central California to southern Oregon. Its more hardy equivalents, among the conifers, extend northward along the coast to Alaska, and occupy the middle levels of the Cordillera, associated with most of the same dicotyledonous genera. As above indicated, a similar forest occupies an extensive area in northeastern Asia.

One of the great physical events of later Tertiary time in western America was the outpouring of extensive and numerous sheets of basaltic and other lavas. The wide areal extent of these flows is itself an indication of relatively low relief over much of Washington, Oregon, and Idaho at the beginning of the Miocene. This eruptive activity has continued down into the Recent, but it reached its climax in the middle part of the Miocene epoch; at that time there were built up the thick series of flows which have formed the Columbia Plateau and which are so well exposed in the gorge of the Columbia River and in its tributary streams of Oregon and Washington. The Lower Miocene sediments underlying these flows have been exposed by the cutting of the John Day and Crooked rivers in eastern Oregon,[21, 22, 23] and the record of the Bridge Creek flora, with its dominant redwood character as above described, has been exposed. During intervals of quiescence between eruptions, there developed a somewhat altered type of forest in Oregon and Washington. This forest, which has been described as the Eagle Creek[24] and the Latah[25, 26] floras, differed from the Bridge Creek in the less dominant position of *Sequoia,* and in the greater abundance of maples, poplars, and such broad-leafed deciduous oaks as *Quercus pseudolyrata.* It is clearly of a more upland type than the flood-plain forest of the Lower Miocene, and appears to have occupied a region of greater relief. Even more definite is the suggestion of the Mascall and other related floras which occur in tuffaceous deposits overlying the Columbia lava, and which are referred to the Upper Miocene. In these later floras, *Sequoia* holds a relatively unimportant position; the dominant types are *Abies, Acer, Aesculus, Arbutus, Betula, Platanus, Populus,* and *Quercus* (both broad-leafed and evergreen types). In such florules as that from Trout Creek in southeastern Oregon[27] and from the Blue Mountains of eastern Oregon,[28] there is definite indication, in the occurrence of *Abies, Amelanchier, Picea,* and *Sorbus,* of an altitude of several thousand feet at the site of deposition. The general character of the Upper Miocene floras has been shown to resemble closely that of the forest now living on the borders of the redwood belt[29] under more exposed and less humid conditions than those of the Bridge Creek flora. The stratigraphic position of these Upper Miocene floras is commonly so well marked, separated as they are from the sediments bearing the Lower Miocene Bridge Creek flora by the thick series of basaltic flows of Columbia lava, that there is little possibility of error in establishing their relative age; and the Upper Miocene vegetation is always of a less mesophytic type than that of the Lower Miocene. The habitat, involving in all probability a more exposed topographic setting, was also characterized by less rainfall and greater extremes of temperature. These physical changes appear to have been caused by the incipience of the orogeny which has subsequently produced the Cascade Range and related structural units in the northern part of the Great Basin, together with renewed uplift of the Sierra Nevada. The effect of these mountains on the climate and vegetation of the areas to the east is too well known to merit description in this paper. It need only be mentioned that they cut off from the interior of western North America the atmospheric circulation which had given it its mild, moist climate; as a result, the redwood and related coniferous forests became confined to the coastal slopes. From eastern Washington and Oregon the more mesophytic elements of the vegetation have gradually been eliminated until they survive only to a limited degree at higher altitudes in protected situations, with *Artemisia* and *Juniperus* occupying the broad expanse of the Great Basin.

The gradual steps by which the humid forest was restricted, not only in North America but also in Asia, are being made known by studies of Pliocene floras on both sides of the Pacific. With the breaking up of the extensive areal units by mountain-making, with resultant diversity in topography and climate, the situations in which plant remains might be preserved became fewer. As a result, the floral record of this latest epoch of the Tertiary is less completely known than the record of those previously discussed. In western America, Pliocene floras are known only from California and Nevada.[30, 31, 32] Except in the coastal region, where a modified redwood forest has persisted down to the present, they are made up, in large part, of trees such as *Alnus, Platanus, Populus, Quercus* (evergreen-oak types), and *Salix,* which occupy stream borders in regions of low rainfall. Another element, comprising *Arctostaphylos, Ceanothus, Cercocarpus, Garrya,* and *Heteromeles,* makes up the first unit of true chaparral that has been recognized in the fossil record. A third element, apparently confined to higher altitudes, includes *Cupressus, Libocedrus, Pinus* (nut-pine type), *Quercus,* and *Robinia,* with the palm, *Washingtonia,* on the adjacent sand washes. Most of these Pliocene species are not only similar in leaf character to modern species of their genera, but they also appear to have occupied essentially the same habitats over the same range. The exotic element, unlike that of older Tertiary floras, is numerically unimportant. A significant example of this element is *Ulmus brownellii,* a species with small leaves having simple-serrate margins, first reported from the lower Miocene of Oregon, and ranging as far east as Colorado before the end of that epoch. Elm leaves of the same characteristic appearance have recently been recorded from the lake beds of Pliocene age in Shansi Province, China,[33] and *U. parvifolia,* the modern equivalent of both fossil species is today widespread in the cooler and drier forested areas of northern China. Here is an example of a tree the leaf characters of which permitted its survival in western America long after most deciduous types, including several species of its own genus, had become extinct, and which has survived down to the present in the somewhat more favorable habitat afforded in northeastern Asia.

As is true of the Pliocene floras of western North America, the known vegetation of this epoch in Asia is essentially like that now occupying the same areas. *Acer, Amelanchier, Picea,* and *Ribes* are among the other genera recorded in Shansi. To the west, in Sinkiang and adjacent provinces of northwestern China, a small but critically important flora has recently been described,[34] all of whose species have closely related living equivalents in central Asia at the present time. The two common trees are a poplar whose leaves are indistinguishable from those of the *Populus euphratica* now occupying river borders and sand washes in the interior of Asia Minor, and an elm that is essentially like *Ulmus pumila,* which occupied the arid portions of central and northern China, including the borders of the Gobi Desert of Mongolia. Associated with the leaf impressions of these and other species of the sand washes and canyons, there have been recorded the remains of an aquatic element which occupied the lake basins in which the sediments were accumulated. Leaves and stems of *Nuphar* and *Typha,* together with grasses and sedges, give a picture not unlike that in many arid and semiarid parts of Asia and North America today, where low precipitation and the consequent reduction in importance of valley development result in the presence of numerous shallow basins at the foot of mountain ranges.

Although the Pliocene floras of both continents show a marked resemblance to the modern vegetation of the same regions, there is apparent in most of them a somewhat less arid aspect than exists at present. The physical conditions characterizing this epoch may be summarized as having involved a topography essentially as diverse as that of today, together with a climate in which high range of temperature and annual rainfall varying from 10 to 20 inches resulted in the development of locally differentiated plant formations with relatively few generic and specific representatives.

The Pleistocene floras of western America have been so recently and adequately described by Mason and others[35, 36, 37, 38] that the present discussion warrants only a brief summary of the plant record for the epoch immediately preceding the Recent. Most of these floras represent coastal vegetation in California that is of essentially the same type as that now living, including a large number of herbaceous species represented mostly by fruiting structures. The most significant difference in the present discussion is that certain of the Pleistocene florules, notably those from Carpinteria and Santa Cruz Island, are made up of species which occupied regions several hundred miles beyond the present southern limits of their range. The extension into southern California of the range of such species as *Cupressus goveniana, Pinus radiata, Pseudotsuga taxifolia,* and *Sequoia sempervirens* may be interpreted as an indication of increased precipitation and lowered temperature quite as definite as the advance of ice sheets from the north. The subsequent withdrawal of these species northward to and beyond the Monterey Peninsula is an equally definite record of a return to southern California of the dry and warm climate which now characterizes it. The relation of the Pleistocene floras of California to the modern coastal closed-cone pine forest, with its present differentiation into floristic units, has been so fully discussed by Mason[35] that it need only be mentioned here.

Pleistocene floras in Oregon, Washington, and British Columbia have not been extensively collected and studied, but those now available indicate the probable existence of differences from those of California which were consistent with the differences in latitude. A small flora from near Fairbanks, Alaska,[39] is made up of *Betula, Salix,* and other boreal types. It may be suggested that in the Pleistocene there was essentially as great diversity in the forests from south to north along the Pacific Coast as now.

The Pleistocene floras of Asia have only recently become an object of study, especially in connection with the occurrence of early man in China.[40, 41] On the basis of our present incomplete knowledge, it may be supposed that they differed only in a small degree from the modern forests of the regions where they have been collected.

In discussing the history of the Cenozoic plants bordering the northern basin of the Pacific, particularly with reference to their stratigraphic sequence and geographic distribution, it has been necessary at various points in this paper to describe and interpret the physical conditions under which they lived. This has been essential because their distribution both in time and in space has been conditioned by physical changes which have resulted in their migrations. The major movements have been southward as a result of a progressive trend toward cooling and aridity since the early Tertiary, but secondary movements in the opposite direction have been detected and have played their part in establishing the character of modern vegetation. The gradual shifting southward of the northern limits of most of the Eocene species has resulted in their restriction to the low latitudes of Asia and America, in the forests of which there is a remarkable correspondence of genera on both sides of the Pacific. Following closely behind them, as successful competitors under changing conditions of climate, the temperate Miocene flora with its dominant *Sequoia* element left the northern regions and became widely established in middle latitudes of both continents. Further modifications have served to eliminate the redwood from most of its former range and have localized the deciduous element on the eastern sides of the continents where summer rains and winter cold are prevalent, or to the higher altitudes of western America where this general climate is duplicated. With the late Tertiary uplift of the Cascade Range and the Sierra Nevada to essentially their present height, and with the consequent development of diversified topography of high relief, the relatively uniform floras of middle Tertiary time have also become diversified, with major differences on either side of the mountain ranges, and with the various minor differences which are apparent in the modern vegetation. A modified type of Miocene forest has migrated as far south as southern Guatemala, where such genera as *Alnus, Arbutus, Crataegus, Cupressus, Myrica, Ostrya, Pinus, Prunus, Quercus,* and *Salix* occupy the highlands above the subtropical vegetation of the lower slopes, thus duplicating the association of these two climatic types which characterized the older Tertiary in Oregon and California some 2500 miles to the northwest.

Profound changes in physical conditions around the northern basin of the Pacific in late geologic time, as shown by the lithology, structure, and areal extent of Cenozoic rocks, have altered the vegetation of this region, especially with respect to its distribution. It seems clear that a consideration of the paleontologic record, as well as of the living plants, forms the basis for any complete understanding of modern vegetation.

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The Origin of the Desert Climax and Climate

By Frederic E. Clements

In the popular mind, the word "desert" calls to memory a vast sandy waste, typified by a picture of the Sahara in the first book of geography. The idea has been further confused by the earlier misconceptions concerning the "Great American Desert" of the Missouri Valley, which was actually a grassland climax (where an unrivaled agricultural development has taken place), and the Great Salt Lake Desert, an alkaline expanse left by the retreat of the lake after glacial times. It is evident that these regions have little in common, apart from the quality of vastness and desolation in human terms. The scientist's usage has naturally been more definite, basing itself in part at least upon the physical factors of rainfall and temperature, but even he has sometimes been misled by climatic relicts that have assumed a new rôle as indicators of disturbance. Cacti in particular have contributed to this result, because they bear the impress of the true desert, but they are often found far beyond its present climatic limits. Extensive areas of grassland badly denuded by overgrazing have also been called desert, such as the Red Desert of Wyoming and the southern San Joaquin Valley. However, the latter does have the warrant of a cover of flowery annuals, found likewise in the neighboring Mohave Desert.

The popular usage finds some justification in the original meaning of the word as "abandoned" and hence uninhabited or uninhabitable. In geographic parlance a desert is a region which has little or no vegetation because of a scarcity of rainfall, and thus is relatively unpopulated; while in ecological terms it is an area marked by a peculiar vegetation or, in places or at times, by an absence of it, with low rainfall and high temperature as causal factors. Though the Arctic tundra is sometimes regarded as a desert, this is clearly a return to the primitive meaning of the word and is warranted neither by vegetation nor by climatic conditions. As a consequence, an accurate and practicable definition of the term apparently must be based primarily upon vegetation and rainfall, with some consideration of the animals and of high temperature during the growing season at least. In brief, a desert climax is one marked by the absence of forest or grassland, a critical deficit in rainfall, and a high potential evaporation caused by excessive heat and often by high winds also.

In applying this test to the vegetation of North America, it becomes clear that the term desert is often loosely employed by ecologist and geographer alike. Thus, the so-called sagebrush desert does not meet the requirements over all or almost all of its extent, and even the more xeric *Larrea* community is desert in only a part of the area concerned. The most effective test is afforded by tracing the boundary of the grassland climax in the Southwest and, when this is correlated with rainfall or, better still, rainfall/evaporation, where this is possible, it provides the best delimitation of desert available today. In general, the isohyet of 5 inches marks the disappearance of grass dominants on the climax level, and thus is the readiest means of setting off the desert climax. Much attention has been given to following this boundary on the ground, but it will suffice here to state that the desert, as characterized by *Larrea, Franseria,* and their typical associates, is confined to the Death Valley, Mohave, and Colorado regions and to a larger but less known area in Mexico. Though small districts of similarly low rainfall occur to the north, there temperature and evaporation are less telling, and the *Larrea* climax is replaced by sagebrush and the latter then by grassland.

It should be clearly recognized that the limits of the desert or *Larrea* climax cannot be drawn with exactness at present, and that no more than a fair approximation will ever be possible. Quite aside from the difficulties arising from the slow fluctuations caused by cycles of varying length and intensity, are those produced by overgrazing and its consequences in a climate where this process is the most destructive to grassland. Hence, the limits of the desert plains and mixed prairie associations must be determined by scattered relicts, which are sought most diligently and with greatest success in the wet phase of the cycle, when they are most in evidence. Moreover, these are the very regions deficient in weather records, and the isohyets are based upon relatively few and recent observations so that they serve only as a general index. However, if it be borne in mind that all climaxes are characterized by broad ecotones, it will be seen that these criteria serve as a practicable basis for circumscribing the desert region.

From the essential nature of climates and climaxes, it follows that deserts usually lie in direct contact with grassland rather than woodland or forest. This is particularly true of the Colorado complex and its wide extension in Mexico, though the detailed relations are there much less known. Since the dominants are typically bushes or shrubs, they may come into touch with another scrub formation, such as the sagebrush on the north or along the middle slopes of bordering ranges, but this is partly at least a consequence of grazing disturbance. The desert is largely encircled by three associations of the grassland formation, namely, the mixed prairie on the northeast, desert plains along the extended eastern boundary, and bunchgrass prairie to the west (Clements, 1920; Weaver and Clements, 1929). The last two are to be considered as climatic differentiations of the mixed prairie, arising from the same causes that led to the development of desert in an originally more or less uniform vegetation. This is indicated by the fact that the desert plains of southern Arizona and northern Mexico today swing north as a border along the Colorado Desert. Hence, the origin of the desert vegetation is inseparably bound up with the disappearance of the grass dominants in the region of desiccation and their realignment in the areas round about.

The typical dominant of the desert climax, *Larrea tridentata,* resembles the sagebrush, *Artemisia tridentata,* in its distribution over an area much wider than that in which it is climax. In the United States it is found from western Texas to the eastern edge of the Great Valley of California but, of all this vast stretch, it is climax only in western Arizona and southeastern California, as well as in Mexico. In the wake of overgrazing, it has spread extensively to replace the vanishing grasses, and today its proper climatic region can only be determined by the presence of relict grasses on the one hand and of its peculiar desert associates on the other. As in various other climaxes, disturbance processes have produced a misleading picture, the true significance of which can be discovered only by turning to the dynamics involved. This demands not merely a proper understanding of the effects of disturbance by man, cattle, and rodents, but likewise an insight into the direction and influence of minor and major climatic shifts. Both bio-ecology and paleo-ecology must be called upon to provide a complete synthesis and to permit a reconstruction of past biomes, as well as to trace the developmental processes active in producing the present vegetation. These are the objects of the present paper.

An effort has been made to marshal all the facts that have a bearing, direct or otherwise, upon the modification of grassland into desert under compulsion of a major climatic change. The primary cause of the latter is to be sought in the elevation of neighboring mountain systems, just as its effects are disclosed in the fossil record of the plants and animals that passed across the changing scene. In order to permit a sharp focus, the existence of a grassland climax as widespread as that of today must be taken for granted. This assumption is well justified by the transmontane occurrence of the great genera of grasses, such as *Stipa, Bouteloua, Sporobolus, Poa, Andropogon,* etc., and attested by an ungulate fauna far more varied than that of the present epoch. While the origin of the prairie climax has a direct bearing upon the present problem, this is a matter of such scope and complexity as to demand separate treatment in the future.

In assembling the evidence from all sources, it is necessary to employ the essential method of paleo-ecology by proceeding from the existing biome to the past, and in this task the relict provides the missing key. These witnesses to past events are of several kinds. Chief among them are the relicts still present in the desert, which are few in the climax itself, but more frequent in the protection of mountains in or bordering upon the region. Much more numerous and also of signal value are what may be termed "transads," plants and animals either present or absent today, but at home in the desert when it was grassland as shown by their presence on both sides of the climatic barrier. Next in significance are the species that occur in the desert and on one side of it, either to the east or to the west. Of similar meaning are the changes that have taken place farther away in the grassland without transforming it into desert. A correlated body of evidence is to be derived from the migration of the desert climax from the Mexican homeland, and the evolution of endemics at this or a later time. The indispensable background for this is the evaluation of fossil horizons of plants from Miocene to Pleistocene, with which must be associated the fossil animals and especially the vertebrates. Finally, behind all these lies the record of great orogenic movements expressed in the slow rise of mountain blocks, the reduced access of rain-laden winds, and the "spiral" desiccation of the regions within the lee of the rising chains. The word "spiral" is employed to characterize the resultant of progressive desiccation and of recurring climatic cycles of varying intensity, of which those of the Pleistocene were among the most pronounced.

Relicts Within the Desert Borders

Of this group the perennial grasses, as dominants of the original climax, are obviously the most significant, while the annuals are of little importance apart from their seral relations. These climax dominants have persisted only as a result of local protection, maintaining themselves in some degree in shallow washes, in sand, or on rocky or northerly slopes, wherever edaphic compensation for climatic drouth was to be found. A number have taken refuge in mountain ranges by virtue of higher rainfall and reduced evaporation. Naturally, the grass genera of southern origin have supplied most of these relicts, though the circumpolar *Stipa, Elymus,* and *Poa* are numbered among them. In the following list, the species are arranged under the associations in which they play major rôles today, accompanied by those of subclimax or seral character. As is to be expected from their nature and proximity, the desert plains exhibit the largest number.

Mixed prairie

Oryzopsis hymenoides
Poa nevadensis
Elymus sitanion
Hilaria jamesi
Bouteloua gracilis
Bouteloua racemosa

Desert plains

Aristida purpurea
Aristida p-wrighti
Aristida divaricata
Aristida d-parishi
Aristida californica
Aristida glauca
Hilaria rigida
Triodia pulchella
Sporobolus cryptandrus flexuosus
Sporobolus wrighti
Muhlenbergia porteri
Muhlenbergia lemmoni

California prairie

Stipa speciosa
Stipa pulchra
Poa scabrella

Coastal prairie

Andropogon saccharoides
Andropogon glomeratus

Seral dominants

Distichlis spicata
Sporobolus airoides
Sporobolus asperifolius
Hordeum jubatum
Phragmites communis
Imperata hookeri

Few of these constitute extensive communities today. *Hilaria rigida* and *Triodia pulchella* are the most important in this respect, and next in order are *Oryzopsis hymenoides, Aristida p-wrighti, Stipa speciosa, Poa scabrella,* and *Distichlis spicata.* The most complete community relicts so far discovered occur in the Avawatz Mountains on the south rim of Death Valley at an altitude of 4300 feet. Here are associated *Hilaria jamesi, H. rigida, Aristida p-wrighti, Stipa speciosa, Poa scabrella, Oryzopsis hymenoides,* and *Sporobolus c-flexuosus,* at their best on rocky north exposures. In sandy plains about the playas in the western part of the Mohave, *Poa scabrella, Oryzopsis, Stipa speciosa, Elymus sitanion,* and *E. cinereus* grow together, and in sandy areas at Goffs and across the Colorado River at Yucca, *Hilaria rigida, Aristida p-wrighti, Muhlenbergia porteri,* and *Sporobolus c-flexuosus* occur. As would be expected, almost all these are southern in origin; they belong to the grass associations that border the desert today and have most recently withdrawn from it. By contrast, such major dominants of the mixed prairie as the two Boutelouas and *Hilaria jamesi* persist only in the mountains, while the boreal *Stipa comata* and *Agropyrum smithi* have moved well to the north.

The presence of two or more dominants from each of four associations out of the six that form the prairie climax denotes that the original grassland of the desert area belonged to a biome much less differentiated than at present. Most wide-ranging of the species concerned are *Bouteloua racemosa* and *Sporobolus cryptandrus,* which extend from the Atlantic to California and from Canada into Mexico; *B. gracilis* and *hirsuta,* with a similar extension from the Middle West; and *Andropogon glomeratus,* which stretches in a broken line from ocean to ocean in the south.*

TRANSADS

These are dominants or subdominants that still exist on both sides of the desert and consequently must have extended through

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* Note: A steady effort has been made to verify and extend recorded ranges both in field and herbarium during the past decade or more, but it is not to be hoped that final accuracy can be attained in this respect. Some early records by competent botanists are no longer verifiable, especially where disturbance has obliterated rare extralimital stations as it seems to have done with *Buchloe* in Canada and Arizona. For the Southwest in particular, ranges have been drawn chiefly from Jepson's Manual for California, Tidestrom's Flora of Utah and Nevada, and Shreve's MS catalogue for Arizona. Sargent's Manual and Sudworth's bulletins have been utilized for the drawing of tree ranges.

it during occupation by the grassland climax, but may or may not occur within its borders today. Here again the grasses are of the first importance, though perennial forbs and woody plants also possess much significance. Strictly speaking, transads are to be regarded as single species, but groups of closely related linneons have similar if somewhat less meaning, and this is also true of certain paired genera. The annuals have value, but it is often difficult to determine, and they receive small consideration, except for the group of desert endemics. Furthermore, hydrophytes and halophytes not only possess peculiar ability to migrate but they also evade climatic control in varying degree. Their presence, therefore, is not of great significance. Finally, a large number of species occur in the higher altitudes of mountains on both sides of the desert, but these have moved from the north along parallel systems and probably have never stretched across the desert region.

In consequence, the species listed below comprise only those of which there is clear evidence that they once extended across some part of the climax desert, as represented by the region from Death Valley southward. There was desiccation to the east all along the Sierra-Cascade axis, but this was not sufficient north of Owens Lake to maintain the *Larrea* desert.

Grass transads still present in the desert

Oryzopsis hymenoides
Stipa speciosa
Aristida divaricata
Aristida d-parishi
Aristida purpurea
Poa scabrella
Poa s-nevadensis
Elymus sitanion
Phragmites communis
Bouteloua gracilis
Bouteloua racemosa
Andropogon saccharoides
Andropogon glomeratus
Sporobolus airoides
Sporobolus asperifolius
Hordeum jubatum
Distichlis spicata

Grass transads no longer found in the desert

Stipa comata
Stipa minor
Stipa eminens
Stipa coronata
Bouteloua hirsuta
Bouteloua rothrocki
Bouteloua radicosa
Aristida p-fendleriana
Elymus triticoides
Koeleria cristata
Epicampes rigens
Bromus marginatus
Andropogon scoparius cirratus
Aristida d-schiedeana
Eragrostis secundiflorus
Panicum huachucae

Several of the grasses named above are dominants of the true prairie, notably *Andropogon scoparius, Bouteloua racemosa,* and *Koeleria cristata.* The last-named retains this rôle through the mixed prairie and into the bunchgrass association of California. In reduced rank, though still as a dominant, *B. racemosa* appears in both mixed prairie and desert plains; *Andropogon* becomes postclimax in both. *Bouteloua rothrocki, B. radicosa* in several forms, and *Aristida d-schiedeana* are dominants of the desert plains, while *Elymus triticoides* is the valley consociation throughout the California prairie.

Forb Transads

Of this group, the perennial species are of chief importance as being more characteristic of climax areas, while the annuals are in large part and often wholly seral. Like the grasses, this group is divisible into those still persisting in the desert and those that have disappeared from it but that survive today on both sides. The latter are generally more mesic than the former, and a number of them, namely, *Erysimum asperum, Glycyrhiza lepidota, Lotus americanus, Verbena hastata,* and *Urtica gracilis,* extend east into the true prairie or farther. There are approximately 70 desert transads, of which 41 are annuals. The transads no longer present in the desert comprise 44, 20 of them annuals. The greater number of annuals in the first group accords with the general rule for the desert. The majority of the perennials extend at least to the western edge of the Great Plains, but the typical societies of the true and mixed prairies drop out long before reaching the borders of the desert, as would be expected.

As may readily be inferred, aquatic forbs afford an exceptionally high percentage of transads; in fact, there are but one or two of this group restricted to the desert and only a few that extend to either side. The number of transads still found in the desert barely exceeds a dozen, and these are almost wholly confined to the sedge family, to *Juncus, Typha,* and the duckweeds. The aquatic transads that have disappeared from the desert are twice as many and their relationships are much wider, the cosmopolitan genera of the figwort family being best represented. Although the inference is plausible that many of these transads have persisted since the remote days of extensive swamp and meadow, the relative ease of migration among aquatics does not exclude more recent colonization. However, they not only aid in completing the details of the reconstructed picture, but they also prove that desert climates do not exclude perennial ponds and swamps with their characteristic water plants and animals. Thus, in desert as in grassland generally, such edaphic compensation for climatic dryness is more or less adequate, if occasional, and the organisms concerned cannot be directly employed as climatic indicators.

SHRUB TRANSADS

These are likewise divided into desert transads and transads proper, the former numbering three times the latter. However, for the present purpose it is more convenient to arrange the members of both groups in accordance with the climax in which they find their chief part. As to origin, by far the greater number are of southern derivation, amounting to 75 per cent. The exceptions are chiefly dominants of the mountain chaparral that are common to the Petran and Sierran associations, such as *Rhus trilobata, Cercocarpus parvifolius* and *ledifolius, Amelanchier alnifolia, Holodiscus discolor,* and *Jamesia americana.* A few such as *Artemisia tridentata, Atriplex canescens, Chrysothamnus nauseosus* and *viscidiflorus, Eurotia lanata, Gutierrezia sarothrae, Sarcobatus vermiculatus,* and *Ribes cereum* range as far north as Canada.

Desert scrub climax

Larrea tridentata
Encelia farinosa
Acamptopappus sphaerocephalus
Haplopappus linearifolius
Dalea californica
Prunus fasciculata
Nolina parryi
Prosopis juliflora
Acacia greggi
Baccharis emoryi
Baccharis glutinosa
Hymenoclea salsola
Hymenoclea monogyra
Pluchea sericea

Sagebrush climax

Artemisia tridentata
Atriplex confertifolia
Atriplex canescens
Chrysothamnus nauseosus
Chrysothamnus viscidiflorus
Grayia spinosa
Eurotia lanata
Sarcobatus vermiculatus
Brickellia californica
Viguiera deltoidea
Zauschneria californica
Pentstemon antirhinoides
Eriodictyum californicum angustifolium
Salvia carnosa

Chaparral climax

Rhus trilobata
Cercocarpus parvifolius
Cercocarpus ledifolius
Ceanothus cuneatus greggi
Amelanchier alnifolia
Holodiscus discolor
Jamesia americana
Arctostaphylus pungens
Arctostaphylus pringlei
Purshia glandulosa

Prosopis and *Acacia* are postclimax, being found typically in washes or valleys along with other treelike species, while *Baccharis, Hymenoclea,* and *Pluchea* are essentially seral. The major dominants of the Basin sagebrush are those listed in the first column; *Sarcobatus* constitutes the subclimax of the halosere, and the remaining species belong to the Coastal sagebrush. As noted earlier, most of the chaparral dominants are northeastern, but *Arctostaphylus* and *Ceanothus* are derived from the Pacific Coast.

TREE TRANSADS

Because of their higher water requirements and more direct exposure to the influence of a changing climate, trees present few simple transads. But three species of this group occur in the desert at this time, namely, *Salix lasiolepis, exigua,* and *Populus fremonti;* the first two are usually shrubs, and all are confined to valleys or washes with higher water-content than that of the desert proper. For similar reasons, the same genera furnish most of the transads no longer present in the desert, such as *Salix levigata, nigra, fluviatilis,* and *Populus trichocarpa.* The other member of this group is *Celtis mississippiensis* in the variety *reticulata.*

PHYLADS AND GENERA

TREES

In addition to single species that cross the desert, there is a much larger number of phylads, that is, phyletic lines of closely related species, that stretch from the Atlantic or the Mississippi Valley to the Pacific. In some of these the relationship is so intimate that the ecologist would regard the forms concerned as subspecies or varieties of a single linneon. This is true of the phylad *Quercus minor-gambeli-garryana,* the last two members of which appear to differ in no important particular. *Quercus minor* and *gambeli* are in close proximity in western Texas; the latter occurs in the mountains of western Arizona and Nevada, and *garryana* extends into the southern Sierra Nevada. *Q. alba* and *lobata* are likewise nearly related, though the present gap between them reaches from central Texas to the edge of the Great Valley in California. A similar lacuna exists between *Q. velutina* and *kelloggi,* which might well be regarded as varieties of the same species.

An even more striking example is afforded by the *virginiana* phylad, of which the primary species ranges from Virginia through the South to Mexico and Lower California, where it meets *Q. dumosa* of central and southern California. *Q. emoryi* of the same group stretches from the mountains of western Texas through those of southern Arizona, and *Q. engelmanni* lies in contact with *dumosa* in southern California and in close proximity to *virginiana.* The phylad *Q. breviloba-undulata-douglasi* is morphologically continuous, the respective ranges being from Alabama to central Texas, western Texas to the eastern border of the desert, and from northern California to the rim of the Mohave. Similarly, in the phyletic line *Q. myrtifolia-hypoleuca-wislizeni-agrifolia,* the first extends from South Carolina to Mississippi, the second from western Texas to Arizona and Sonora, and the third from desert slopes to Lower California and northward, often meeting *agrifolia* in southern California.

Phylads of similar significance in respect to evolution and migration are exhibited by *Juglans, Fraxinus, Platanus, Populus, Pinus,* and *Juniperus,* as well as by the more shrublike *Arbutus, Aesculus,* and *Prunus. Juglans nigra-rupestris-californica* is essentially a structural continuum, and from Massachusetts to California is interrupted only by the desert. The continuity in both respects is even greater, if possible, in *Fraxinus americana-texensis-velutina-coriacea-oregona;* the first two overlap in Texas; *velutina* reaches from Texas to Inyo County, California; *coriacea* occurs in the desert region from southern Utah to southeastern California, and *oregona* from the mountains of southern California to Washington. *Platanus occidentalis-wrighti-racemosa* extends from New England to southern and Lower California, touching the borders of the desert on both sides. *Populus deltoidea* and *fremonti* meet in southern Colorado and western Texas to span the continent, and the closely related *wislizeni* overlaps them both in Texas and New Mexico.

Though best regarded as one polymorphic species consisting of *monophylla, edulis, cembroides,* and *quadrifolia,* with complete overlapping in the needle number, the pinyon is usually treated as four. *Pinus edulis* ranges from Utah and Colorado to western Texas, Arizona, and northern Mexico; *cembroides* through the southern half of Arizona and adjacent Mexico to Lower California; *quadrifolia* from Lower California to the arid Santa Rosa Mountains along the Colorado Desert, and *monophylla* from northeastern Utah to Nevada, northern Arizona, and the southern Sierras into Lower California. *Juniperus utahensis* and *californica* meet today in southeastern California, while the general areas of *monosperma* and *occidentalis* confront each other over a long line.

Arbutus menziesi makes its home from British Columbia to the mountains of San Diego County, California; it is separated by the desert from *A. arizonica* in southern Arizona and Chihuahua, where *A. arizonica* is in proximity to *A. xalapensis* of Mexico and Texas. *Aesculus californica* reaches the margin of the Mohave in Antelope Valley; its cognates are *glabra* and *octandra,* which range from Pennsylvania to Oklahoma and to western Texas, respectively. The wide interval is occupied in part by the related monotypic *Ungnadia speciosa* of Texas, New Mexico, and northern Mexico. *Prunus nana-melanocarpa-demissa* is found from Newfoundland to California, the widespread *melanocarpa* overlapping the limits of the other two.

Less definite though still suggestive evidence of former continuity across the desert is presented by a number of paired genera, such as *Castanea-Castanopsis, Catalpa-Chilopsis, Persea-Umbellularia, Sabal-Washingtonia, Taxodium-Sequoia,* and *Aesculus-Ungnadia,* as already mentioned. In each pair the eastern genus finds its western limits in Texas, except *Catalpa,* which stops in Mississippi; while the western genera are confined to California or the Pacific Coast, except *Chilopsis,* which reaches the lower Rio Grande, and *Ungnadia,* which ranges from eastern Texas to New Mexico and Mexico.

SHRUBS

Several phylads of this group cross the continent almost without interruption, though it is a pertinent question whether each of these is not a single species. *Sambucus canadensis* ranges from New Brunswick to Colorado and Texas; it gives way in New Mexico to *mexicana,* which reaches California and there meets the closely related *glauca. Cercis canadensis-reniformis-occidentalis* is unique in that all three members occur in Texas, *reniformis* being the intermediate both morphologically and geographically. *Vitis* exhibits a phylad of even greater continuous area: *girdiana* extends from coastal southern California into the deserts, *californica* grows throughout the state, *arizonica* occurs from Arizona to west Texas, and *aestivalis* from Texas along the Gulf and Atlantic Coasts. *Staphylea* and *Styrax* are likewise transcontinental, but with a wide gap in the mountain region.

Staphylea trifolia is found from Quebec to Kansas, while *bolanderi* is restricted to central and northern California; *Styrax californica* is more southern, and the limits of *pulverulenta* are from Virginia to Texas. Both forms of *Amorpha* occur over the wide area from New Mexico to California, *fruticosa* reaching southern Pennsylvania and *californica* the San Francisco Bay region.

The remaining phylads are western, *Philadelphus lewisi* occuring from southern California to British Columbia, and *microphylla* from Arizona to Colorado. *Zauschneria californica* ranges from California to Nevada, and *arizonica* from California through Arizona to southwestern Colorado. *Eriodictyum californicum* extends from southern Oregon through central California, *crassifolium* southward to the border, *trichocalyx* along the Cross Ranges to the Santa Rosa Mountains at the west side of the desert, and *californicum angustifolium* from the east side through southern Nevada and Arizona to New Mexico. *Ephedra californica* of the southern part of the state meets *trifurca* in the Mohave and Colorado deserts, and *trifurca* stretches east to Texas and Colorado, sharing the area east of the desert with *torreyana*.The more restricted *Crossosoma bigelovi* occurs from central Arizona across the desert to Lower California, while *californica* is confined to islands off the southern coast.

Species of the Desert and Eastward or Westward

FORBS

The number of species found both in the desert and eastward into the desert plains or mixed prairie is 89; of these, 49 are annuals, 39 of which extend as far east as New Mexico, Colorado, or Texas. Almost all the perennials likewise stretch far to the east, and the majority constitute societies in the mixed prairie of the Great Plains. It appears probable that most of the species of the desert-eastward group originated in the two prairie associations just mentioned and found their western limit at the desert's edge, though some may well have extended into it or even have arisen during its development. The species that occur in the desert and westward through more or less of cismontane California number 91; 67 of these are annuals, 60 of which are found more widely outside the desert. Nearly all the desert-westward perennials appear to be endemic, while the desert-eastward ones are chiefly migrants from the east, as already suggested; 7 likewise occur in Mexico.

SHRUBS

The total of desert-eastward shrubs is 43, 21 of which extend well to the east into Colorado or Texas. Of the westward group of 20, the large majority are endemic, only 4 being found also in Mexico; while of the eastern, 15 occur in Mexico and may well have originated there.

DESERT ENDEMICS

The word endemic is used in a general sense to apply to the desert region as a whole, with full recognition of the fact that the limits of the desert are most uncertain in Mexico and Lower California and none too definite in any direction other than west. On this basis, the group comprises 89 species of annuals, 78 perennials, and 69 shrubs, the total amounting to 236, in contrast to the 247 species found in the desert but also extending into the climaxes on either side. Of endemic annuals, the largest numbers per genus are found in *Phacelia, Cryptanthe, Gilia, Euphorbia, Langloisia,* and *Mentzelia;* among perennials, *Astra-*

galus exceeds all others, with *Aster* and *Sphaeralcea* next. *Opuntia, Dalea,* and *Salvia* lead in the number of shrubby species, followed by *Eriogonum, Brickellia, Atriplex,* and *Echinocactus.*

Differentiation of the Colorado and Mohave Floras

Though both deserts belong to the *Larrea-Franseria* climax, they exhibit a noteworthy difference in genera and species. This is evidently caused by the San Bernardino Range and its continuation to the Colorado River. This serves as a definite physical barrier, though it is not insuperable, and its eastern flank is readily turned. It is also a climatic obstacle to some degree, as was especially true during wet phases, and is in part a causative factor in the not inconsiderable climatic differences between the two regions. Of endemics as defined above, the Mohave contains 90, the Colorado 57, and 89 are common to both; most of the common element may antedate the separation of the deserts, but part of it probably has been caused by climatic pulsations and the resulting migrations. In contrast, Death Valley with two wide entrances has a mere half-dozen strict endemics and only a few more that it shares with the regions round about.

With respect to the total number of species according to life form, 5 grasses are found in the Mohave that do not occur in the Colorado, 4 show the reverse relation, and 17 are present in both. There are 138 forbs in the Mohave, 69 in the Colorado, and 157 are common to both; in the same order, the shrubs number 51, 43, and 59. As would be expected, neither the few grasses nor the many forbs produce much visible difference. This is likewise true of the shrubs and low trees over the general climax area, but these do afford conspicuous contrasts through valleys and washes and along mountain slopes and alluvial fans. In spite of the smaller number of woody species, these often give a distinctive character to the Colorado Desert. The most notable are *Washingtonia filifera, Cereus giganteus, Fouquiera splendens, Parkinsonia torreyana, Olneya tesota, Dalea spinosa, Beloperone californica,* and *Simmondsia californica.* It is understandable that these are all of southern derivation, while the Mohave has obtained most of its important shrubs from the west, north, and especially the east. Even the Joshua tree (*Yucca brevifolia*), though characteristic, is not a strict endemic.

FOSSIL PLANTS

As is well known, grassland and desert do not afford ready opportunity for the production of plant fossils, partly because leaves and stems are not easily detached, but chiefly for the reason that water bodies are relatively few in those regions. The paucity of fossils is naturally more pronounced in desert than in grassland and, so far as the climax desert is concerned, amounts to almost complete absence from the Pleistocene up to the present. Conditions were more favorable on both counts during the Pliocene and still more so in the Miocene, with the result that the fossil floras are increasingly better known for these periods of greater rainfall. Hence, in scrutinizing the evidence of the course of development, it is desirable as usual to proceed from the present and thus to consider the Pleistocene horizons first. The value of these depends in large measure upon proximity, apart from number of species; those in southern California come first, none being found in the true desert so far; those farther north demand more interpretation in terms of difference of climate and vegetation.

Although the general practice of paleo-botany is to provide a separate name for a fossil species, even though it is regarded as probably identical with a modern one, it facilitates comparison and interpretation to employ the name of the existing representative, and this plan is accordingly pursued.

The stations from which Pleistocene fossils have been recorded in California are as follows: (1) Rancho La Brea, in the suburbs of Los Angeles; (2) Carpinteria, near Santa Barbara; (3) Santa Cruz Island, one of the Santa Barbara group; (4) San Bruno, on the west shore of San Francisco Bay; (5) Tomales Bay, not far north of the last-named. As would be expected, the poorest collection is from the first locality and the richest from the last, though edaphic conditions largely determine this for the intermediate stations. The grouping below is approximately into trees, shrubs, and herbs, though the limits of the first two are far from precise.

PLEISTOCENE

RANCHO LA BREA

Trees—	*Shrubs—*	*Herbs—*
Pinus tuberculata	Celtis mississippiensis	Xanthium calvum
Cupressus macrocarpa	Celtis reticulata	
Juniperus californica		
Sambucus glauca		
Quercus agrifolia		

CARPINTERIA

Pinus muricata	Pirus rivularis ?	Pteris aquilina
Pinus radiata	Arctostaphylus glauca	Chorizanthe pungens
Pinus remorata	Ceanothus thyrsiflorus	Cymopterus litoralis
Pinus sabiniana	Garrya elliptica	Corethrogyne filaginifolia ?
Pseudotsuga taxifolia	Rhus diversiloba	
Sequoia sempervirens	Eriodictyum californicum	Xanthium calvum
Cupressus goveniana	Myrica californica	Arceuthobium campylopodum
Juniperus californica		
Quercus agrifolia		
Umbellularia californica		
Sambucus glauca		

SANTA CRUZ ISLAND

Pinus remorata	Arctostaphylus sp.	Arceuthobium campylopodum
Pseudotsuga taxifolia	Ceanothus thyrsiflorus	
Cupressus goveniana	Cornus pubescens	
Myrica californica		

PLEISTOCENE
(*Continued*)

San Bruno

Trees—
- Pseudotsuga taxifolia
- Sambucus glauca

Shrubs—
- Ceanothus thyrsiflorus
- Rhus diversiloba
- Symphoricapus albus
- Rubus parviflorus
- Baccharis pilularis
- Prunus emarginata

Herbs—
- Micromeria chamissonis
- Galium sp.
- Silene sp.
- Montia perfoliata
- Hemizonia virgata
- Rumex salicifolius
- Rumex persicarioides
- Equisetum sp.
- Carex sp.
- Sparganium eurycarpum

Tomales

- Pseudotsuga taxifolia
- Picea sitchensis
- Torreya californica
- Pinus muricata
- Pinus radiata
- Cupressus goveniana
- Acer macrophyllum
- Alnus rubra
- Arbutus menziesi
- Quercus agrifolia
- Umbellularia californica
- Myrica californica
- Sambucus glauca

- Arctostaphylus columbiana ?
- Ceanothus thyrsiflorus
- Ceanothus rigidus
- Garrya elliptica
- Baccharis pilularis
- Adenostoma fasciculatum
- Rhus diversiloba
- Amelanchier alnifolia
- Cornus californica
- Corylus rostrata californica
- Prunus emarginata
- Prunus subcordata
- Rubus parviflorus
- Rubus spectabilis
- Rubus vitifolius
- Symphoricarpus albus
- Vaccinium ovatum
- Arctostaphylus uva-ursi

- Pteris aquilina
- Fragaria californica
- Montia perfoliata
- Galium californicum
- Eriophyllum s. artemisifolium
- Calandrinia caulescens
- Atriplex hastata
- Daucus pusillus
- Camassia leichtlini
- Rumex salicifolius
- Rumex occidentalis
- Rumex maritimus
- Carex spp.
- Scirpus spp.
- Montia howelli
- Montia sibirica
- Montia fontana
- Oenanthe sarmentosa
- Ruppia maritima
- Arceuthobium campylopodum ?
- Datisca glomerata

A detailed consideration of the significance of the species in each flora and of the climatic implications of the flora has been given by the several authors, namely, Frost (1927), Chaney and Mason (1933, 1930), Potbury (1932), and Mason (1934). For the present purpose, the most important fact is their essential agreement that the entire stretch was more humid and correspondingly cooler during the Pleistocene than it is at present, though with the logical inference that this applies to the wet rather than the dry phases of the several cycles. The second value of the lists is to be derived from the general agreement in respect to important dominants, together with their sharp reduction inland at the south. The reference of these dominants to the present climaxes of California furnishes the basis for testing the reconstruction of the successive climaxes that have moved over the desert region from the Miocene to the present.

PLIOCENE

Ricardo: Last Chance Gulch

Woodland—
Pinus cembroides monophylla
Cupressus arizonica ?
Washingtonia ? filifera
Quercus agrifolia

Chaparral—
Robinia neo-mexicana

Alturus-Pico

Coniferous: Coast-montane—
Sequoia sempervirens
Pseudotsuga taxifolia
Pinus lambertiana
Libocedrus decurrens
Pinus muricata
Ribes nevadense
Berberis aquifolium
Smilax californica
Pteris aquilina
Wooodwardia radicans

Woodland—
Quercus agrifolia
Quercus douglasi
Quercus chrysolepis
Quercus tomentella
Castanopsis chrysophylla
Umbellularia californica
Aesculus californica
Arbutus menziesi
Pinus sabiniana

Chaparral—
Cercocarpus parvifolius
Amelanchier alnifolia
Prunus demissa
Garrya fremonti
Heteromeles arbutifolia
Rhus laurina
Ceanothus integerrimus

Seral—
Populus trichocarpa
Populus fremonti
Salix lasiolepis
Salix exigua
Platanus racemosa
Alnus rhombifolia
Fraxinus oregona

In evaluating the Ricardo group, Webber (1933:134) states that all the species are possibly identical with those living now in the general region, but that differencees in range justify their assignment to the Pliocene. Today, the closest approach to the grouping and the related climate is to be found in the San Jacinto Range bordering the Colorado Desert, where palms occur on the desert level, with pinyons and live oaks on the slopes toward the desert. The conclusion is reached that the climate was less extreme than that of the present desert.

The evidence from the other Pliocene horizons of California is indirect because these are much more northerly, except the very scanty remains from the Pico of Ventura (Dorf, 1933:66). The several floras show a close relationship to the living forests of the region, modified somewhat by the effects of a major climatic cycle. It is assumed that the climate of the Lower Pliocene was rather drier and warmer than the present one, but that conditions became cooler and more humid in the Upper Pliocene than they are in the same districts today. Since the Ricardo is regarded as Lower Pliocene, it is clear that the conclusions are not in accord, though this discrepancy may be explained by topographic control. However, there is distinct agreement that the climate of California was drier throughout the Pliocene than during the Miocene.

MIOCENE

Genera common to the Mascall and Florissant

Deciduous climax—	*Coniferous climax—*	*Seral or marginal—*	
Acer	Sequoia	Ulmus	Vitis
Castanea-Castanopsis	Libocedrus	Juglans	Celastrus
Quercus	Pinus	Betula	Ptelea
Fraxinus		Populus	Hydrangea
Liquidambar		Salix	Odostemon
Magnolia		Sapindus	Rosa
Carpinus		Sorbus	Apocynum
		Crataegus	Typha
		Amelanchier	

These two floras have but two species in common, or six if those in the related horizon of Yellowstone Park are taken into account. However, this fact is of little significance, chiefly because the Mascall of the John Day and Trout Creek have been critically reworked by Chaney (1925) and MacGintie (1933) on the basis of the newer ecological technique, while the Rocky Mountain floras yet await such scrutiny. Furthermore, whatever element of doubt may reside in species based upon leaf impressions, this is largely resolved in respect to genera. Consequently, it is logical to assume that both regions exhibited essentially the same deciduous and coniferous climaxes, and that these stretched more or less continuously between the two regions in their respective habitats, while the plateaus and plains were occupied chiefly by grassland and scrub. The continuity of forest was doubtless greater in the Eocene because *Fagus, Castanea,* and *Tilia* were present both in the Rocky Mountains and the Pacific Slope, the intervening shrinkage of forest and extension of grassland being promoted by conditions during the Oligocene of the interior.

Fossil Animals

The carnivores and insectivores are omitted from the following lists for the various formations, primarily because they bear no direct relation to vegetation as food supply. This is likewise true of the raptores among birds. As dwellers in seral habitats, water birds possess little or no value as climatic or climax indicators for grassland or desert and, in this respect, the value of such ground forms as quail, meadowlark, and turtle dove is none too definite (see Grinnell, 1914, 1923, for the birds of Death Valley and the Lower Colorado).

Naturally, the major interest inheres in the ungulates because of the direct response of teeth to type of food and of feet to surface and cover (Kowalevsky, 1873; Osborn, 1910:238). The proboscideans are less satisfactory indicators, and the rodents are significant chiefly in connection with the food coactions and soil reactions that the same species or genera exhibit in the modern biome.

PLEISTOCENE

The selection of the following formations during the three periods of the Pleistocene, Pliocene, and Miocene has been determined in large measure by position in the desert region, or proximity to it, or location in a climate similarly the result of mountain-making processes. The number of genera represented has also been a consideration of importance, though not sufficient to warrant including the rich faunas of the Potter Creek and Samwel Caves of northern California, which belong in a climate of much higher rainfall. For the reasons already given, the water birds are omitted except for the McKittrick area, where they are included for the purpose of suggesting the animal members of the water community in the Pleistocene (see Grinnell, 1923:54–60).

LAKE MANIX

MAMMALS

Ungulates—
Equus, large
Equus, small
Camelops ? large
Camel, small
Antilocapra

Proboscideans—
Elephas or Mastodon

BAUTISTA CREEK

MAMMALS

Ungulates—
Equus
Tapirus
Camelid
Antilocapra
Odocoileus
Capromeryx

McKittrick

MAMMALS

Ungulates—
Equus occidentalis
Camelops
Camel
Bison sp.
Antilocapra ?

Proboscideans—
Mastodon sp.

BIRDS

Ground forms—
Lophortyx californica
Zenaidura macroura
Oxyechus vociferus
Geococcyx californianus
Corvus corax

Water forms—
Podilymbus podiceps
Anas platyrhynchos
Mareca americana
Nettion carolinense
Querquedula cyanoptera
Spatula clypeata
Dafila acuta
Marila americana
Erismatura jamaicensis
Chen hyperboreus
Branta dickeyi
Jabiru mycteria
Ardea herodias
Grus canadensis
Rallus virginianus
Recurvirostra americana
Macrorhamphus griseus
Totanus melanoleucus
Pelidna alpina

Rancho La Brea

MAMMALS

Ungulates—
Equus occidentalis
Camelops hesternus
Bison antiquus
Bison latifrons
Antilocapra americana ?
Odocoileus hemionus ?
Capromeryx minor
Platygonus sp.

Proboscideans—
Elephas imperator
Elephas columbi
Mastodon americanus

Rodents—
Lepus californicus bennetti
Sylvilagus bachmani cinerascens
Sylvilagus audoboni sanctidiegi
Citellus beecheyi fisheri
Dipodomys agilis agilis
Thomomys bottae pallescens
Neotoma intermedia intermedia
Neotoma fuscipes macrotis
Perognathus panamintinus brevinasus
Perognathus californicus californicus
Peromyscus maniculatus gambeli
Peromyscus californicus insignis
Peromyscus eremicus fraterculus
Microtus californicus neglectus
Reithrodontomys megalotis longicaudus
Onychomys torridus ramona

RANCHO LA BREA
(Continued)

Ground forms— Lophortyx californica ? Parapavo californicus Columba fasciata Zenaidura macroura Otocoris alpestris Agelaius gubernator	BIRDS Xanthocephalus xanthocephalus Geococcyx near californianus Sturnella neglecta Corvus corax Corvus brachyrhynchus
	CARPINTERIA
	MAMMALS
Ungulates— Equus near occidentalis Camelops ? cf. hesternus	Odocoileus sp. Bison ? sp.
Rodents— Lepus near californicus Sylvilagus bachmani Dipodomys sp. Thomomys near bottae Neotoma sp. Microtus californicus	Perognathus sp. Peromyscus sp. Onychomys ? sp. Eutamias sp. Sciurus sp.
	BIRDS
Ground forms— Lophortyx californica Parapavo californicus Columba fasciata Turdus migratorius	Geococcyx californianus Corvus corax Corvus caurinus Sturnella neglecta
	FOSSIL LAKE
	MAMMALS
Ungulates— Equus pacificus Camelops kansanus ? Camelops vitakerianus	Antilocapra sp. Camelus maximus Eschatius conidens
Proboscideans— Elephas imperator	Elephas columbi
Rodents— Thomomys sp. Geomys sp. Microtus sp. Lepus townsendi	Ondatra oregona Castor sp. Castoroides sp.
	BIRDS
Ground forms— Tympanuchus pallidicinctus Palaeotetrix gilli	Pedioecetes phasianellus Pedioecetes nanus

Of the six formations considered, only the Manix falls within the desert proper, being more or less central in the Mohave. The Bautista is scarcely beyond the western end of the Colorado. In summing up the evidence for the Manix, Buwalda concludes that the climate in the region and to the west was less arid than at present (1914:457). As to the Bautista, at present this region is grassland under a rainfall thrice as great and hence the difference between Pleistocene and modern conditions was probably less. The mammals of the McKittrick, which is in the "desert" of the upper San Joaquin Valley with a rainfall of 6 inches, are nearly identical with those of the Manix; the genera are all found in the Rancho La Brea and all but one at Fossil Lake, Oregon, indicating a general similarity of climate over this wide range.

The ungulates of Rancho La Brea suggest conditions not much unlike those of the present; the antelope and deer are still found in the general region, and within the historical period both the bison and the reintroduced horse thrived in grassland of less rainfall. Dice (1925:123) believes that the similarity in the rodents indicates that there could have been no considerable or widespread difference in climate between the Pleistocene and the present. On the contrary, Miller thinks that the evidence from the birds, though inconclusive, points to a warm moist climate during the glacial period (1925:70). Hay reaches the conclusion that the Brea deposits were laid down in the Aftonian interglacial stage of the early Pleistocene, when the climate was warm (1927), though this term may well be relative to the Nebraskan and Kansan glacial stages that preceded and followed. The indications at Carpinteria are essentially the same as at Rancho La Brea, and at both places the rodents and ground birds are nearly all those of the present (Wilson, 1934; L. H. Miller, 1931; A. H. Miller, 1932).

Though noting the differences between the faunas of Rancho La Brea and Fossil Lake deposits, Hay concludes that those of the latter also belong to the Aftonian (1927:191), in spite of the indications that it was more desert-like and colder. It seems probable that these and other discrepancies already noted are to be explained by smaller differences in the climates of the Pleistocene of the Far West and less clearly marked limits between glacial and interglacial stages. When allowance is made for the wet and dry phases of the climatic cycles, it appears that the latter half of the Pleistocene differed little from the present over the vast stretch of the grassland climax.

PLIOCENE

Ricardo

MAMMALS

Ungulates—
Hipparion mohavense
Hipparion spp. 2
Pliohippus tantalus
Pliohippus fairbanksi
Pliohippus sp.
Procamelus spp. 2
Pliauchenia sp.
Alticamelus ? sp.
Merycodus near necatus
Merycochoerus ? californicus

Proboscideans—
Tetrabelodon ? sp.

Rodents—
Lepus ? sp.

Thousand Creek

MAMMALS

Ungulates—
Pliohippus ? sp.
Equus ? sp.
Camel, cf. Camelus americanus
Pliauchenia ? sp.
Sphenophalis nevadensis
Ilingoceros alexandrae
Ilingoceros schizoceras
Teleoceras ? sp.
Prosthennops ? sp.

Proboscideans—
Tetrabelodon ? sp.

THOUSAND CREEK

MAMMALS

(*Continued*)

Rodents—
Lepus vetus
Citellus sp.
Peromyscus antiquus
Peromyscus sp.
Arctomys (Marmota) nevadensis
Arctomys (Marmota) minor
Aplodontia alexandrae
Diprionomys parvus
Diprionomys magnus
Entoptychus minimus
Mylagaulus monodon
Eucastor lecontei
Dipoides sp.

BIRDS

Branta sp.

RATTLESNAKE

MAMMALS

Ungulates—
Pliohippus spectans
Hipparion sinclairi
Hipparion occidentale
Hipparion leptode ?
Hipparion anthonyi
Pliauchenia ? or Alticamelus
Sphenophalos sp.
Ilingoceros or Sphenophalos ? sp.
Teleoceras ? near fossiger
Prosthennops ? sp.
? Platygonus rex

Proboscideans: remains—

Rodents—
Otospermophilus gidleyi
Lepus (Hypolagus) vetus

The three Pliocene formations considered comprise a wide extent of territory in the lee of the rising mountains, from the Mohave Desert at the south to northwestern Nevada and eastern Oregon. In spite of a difference of several degrees of latitude, the ungulate faunas have much in common, the significant fact being the predominance of advanced types. Merriam has characterized the Ricardo region as follows (1919:526):

> The Ricardo fauna suggests climatic conditions permitting the development of vegetation suitable for grazing animals. This indicates a somewhat heavier growth of grass than is found in this region at the present time. There is nothing in the constitution of the fauna to suggest conditions radically different from those obtaining today, but the presumption is in favor of less extreme aridity than is now known on the western border of the Mohave Desert. The conditions

prevailing in this region in Ricardo time were probably not widely different from those now obtaining in the southern portion of the Great Valley of California.

The same authority states that the mammals of Thousand Creek suggest plains with meadows or occasional lakes; the rainfall may have been somewhat higher and the temperature rather lower than at present (1911:219). Merriam, Stock, and Moody (1925:59) make no statement concerning the vegetation and climate of the Rattlesnake formation, but the comparison with the Ricardo and Thousand Creeek clearly indicates that these three must have been much the same throughout, the more advanced character of the Rattlesnake being offset by the southern position of the Ricardo.

In support of the assumption of a widespread prairie climax during the Pliocene may be adduced the occurrence of the major grazing genera in the Middle West. Three species of *Hipparion* are recorded for the Snake Creeek of northwestern Nebraska, two for Florida, and one for the Blanco of Texas. The Blanco also exhibits one species of *Pliohippus;* the Clarendon of the same state, two species; the Snake Creek, three; and South Dakota horizons, two. The Snake Creek and neighboring Valentine contain two species of *Procamelus,* and the former has one species of *Pliauchenia.* Of *Merycodus,* the Snake Creek has one form, the Valentine two, and the Santa Fe of New Mexico two.

MIOCENE

BARSTOW

Ungulates—
Hypohippus near affinis
Parahippus ? mourningi
Merychippus (Protohippus)
Merychippus intermontanus
Merychippus calamarius stylodontus
Merychippus sumani
Protohippus ? or Pliohippus ?
Procamelus spp. 2
Pliauchenia sp.
Merycodus ? coronatus
Merycodus necatus ?
Dromomeryx or Cervus ? sp.
Prosthennops ? sp.
Alticamelus ? sp.

MIOCENE

BARSTOW

(*Continued*)

Proboscideans—
Tetrabelodon ? sp.

Rodents—
Lepus ? sp.

Virgin Valley

Ungulates—
Hypohippus near osborni
Parahippus cf. avus
Merychippus mesonesus
Camel, near Procamelus
Aphelops ? sp.
Moropus ? sp.
Merycodus near furcatus
Merycodus near nevadensis
Dromomeryx ? sp. near borealis
Dromomeryx ? sp.
Blastomeryx mollis
Merychyus ? sp.
Thinohyus ? sp.

Proboscideans: remains—

Rodents—
Lepus vetus
Palaeolagus nevadensis
Aplodontia alexandrae
Mylagaulus monodon
Mylagaulus pristinus

The faunistic data for the transmontane area during the Miocene are derived from the same localities as are those of the Pliocene; they are represented by the Barstow, Virgin Valley, and Mascall. These are reënforced by the Cedar Mountain deposits near Walker Lake in western Nevada, which closely resemble the first two, particularly in the ungulates. According to Merriam (1919:450), the Barstow fauna denotes an open country with much grass and herbage, better watered than the present desert. The abundance of *Merychippus,* merycodonts, camels, and related forms, indicates that grasses were well represented and hence that the climax must have been grassland. The climate was probably semiarid, like that of parts of the Great Valley today. Likewise, the horses, camels, and merycodonts of Cedar Mountain suggest a semiarid climate not greatly different from that of the region at present, but the other forms are regarded as indicating a slightly more humid climate with savannah and chaparral such as now occur around the margin of the Great Valley (Merriam, 1916:168).

In discussing the Virgin Valley fauna, the same author (1911: 206) concludes that the closest relationships are with the Mascall of Oregon and the Pawnee Creek of Colorado, though the similarity with the Snake Creek beds of northwestern Nebraska is actually greater. Here again, the ungulates provide the significant evidence, and leave little question that the Great Basin and Middle West were peopled in large part by grazing types living in a climax of mixed prairie, but probably without the short-grasses of today.

Deformation and Climatic Cycles in the General Region

A comprehensive account of deformational and climatic cycles, with particular relation to changes of climax and the significance of the climax sere or clisere, has been given in Plant Succession (1916: 304, 321, 364). The geological materials for this were drawn chiefly from Chamberlin and Salisbury (1906) and from Schuchert (1910, 1914). In scrutinizing the earlier conclusions in respect to the climate of the desert region, further data have been taken from Schuchert (1924), Jones, Antevs, and Huntington (1925), and Antevs (1929).

For the present purpose, the deformation cycles of direct import are three, namely, Paleocene-Lower Oligocene, Upper Oligocene-Miocene, and Pliocene-Pleistocene, forming the long interval from the disappearance of the Cretaceous Mediterranean to the present. The immediate consequence of each cycle was a primary climatic pulsation, in which were involved smaller ones caused in all probability by solar fluctuations. The best known and most pronounced of these were the glacial-interglacial alternations more recently regarded as five in number, the glacial phases known as Nebraskan, Kansan, Illinoian, Iowan, and Wisconsin, with the four interglacial ones. There is also increasing evidence of smaller cycles, such as can be discerned in varves, tree rings, and other phenomena, but none of these was sufficiently long to lead to the evolution or mass migration of a climax.

The Paleocene deformation appears to have been greater in the region of the Rocky Mountains than along the Pacific, with its effect to be seen in a warm-temperate deciduous forest, while the Pacific area was clothed with a subtropical forest (Chaney, 1933). In the long quiescent period of the Eocene and Lower Oligocene, swamp sedges and grasses seem to have spread widely over the interior of the continent, as indicated by the presence of such genera as *Carex* and *Phragmites* in the Cretaceous. It is probable that the evolution of grassland proceeded more rapidly in the period of mountain-making in the Upper Oligocene to produce the forerunner of the modern prairie in the Miocene, where the typical genus *Stipa* is recorded, along with horses of the grazing type, *Merychippus* and *Protohippus*. It is a plausible assumption that, by the time of the Miocene, grassland had become the distinctive climax in at least the central and southern parts of the Great Plains and had spread westward through the present desert, as attested by the ruling abundance of *Merychippus* in the Barstow and the appearance of a still more advanced grazing type, *Protohippus* or *Pliohippus* (Merriam, 1919:479). With the rise of the Cascadian axis in the late Miocene, this dominance of prairie must have been gradually extended, probably with the general replacement of tall subtropical grasses by the northern mid-grasses and western short-grasses.

The general trend toward desiccation in climate and climax may well have found its chief expression at the time of greatest elevation of the Sierra Nevada and Cross Ranges in the Pleistocene, to be succeeded by the four or five glacial cycles already mentioned. If the interglacial phases were long, it is plausible that desert conditions similar to those of today intervened more than once, though the secular trend of rainfall as well as the grass relicts still found in the desert, particularly in Death Valley, suggest that today constitutes at least one maximum. This view is supported by the presence of two horses, two camels, a large antelope, and a probable elephant from Lake Manix, indicative of at least a fairly continuous grass-cover as late as this deposit.

As to the particular times of mountain-making that produced the desiccation of the grassland climate which finally terminated in the desert climate and climax, Hershey places the structural differentiation of the Sierra Madre-San Bernardino chain at the opening of the Quaternary, concluding that the great bajadas were finished by the Illinoian or Iowan stage. Baker (1911) thought it probable that deformation immediately preceded or coincided with the formation of the Rosamond (Barstow) deposits of the Upper Miocene, and that an arid climate like that of today prevailed during this time. An interval of diastrophism then intervened, followed by a long period of erosion which was succeeded by a time of mountain-making that produced the present ranges of the desert. Knopf (1916) concludes that the latest major uplift of the Sierra Nevada occurred early in the Pleistocene, but Blake (1914) regards the end of the Pliocene as the time of uplift in the Colorado region. Merriam (1919) considers the Ricardo beds to be derived from a Sierra range that, in late Tertiary, rose several thousand feet above the floor of the Mohave Desert. Recently, Blackwelder (1931) has studied the eastern slope of the Sierra Nevada to determine the times of Pleistocene glaciation and has constructed a tentative table of glacial stages in the western United States, in which the four recognized in the Sierran region, namely, McGee, Sherwin, Tahoe, and Tioga, are correlated respectively with the Nebraskan, Kansan, Iowan, and Wisconsin of the Middle West.

RECONSTRUCTION OF THE CLISERE OR SERIES OF CLIMAXES

Methods.—The concepts and methods of paleo-ecology were first developed in Plant Succession (1916:344–362) and were recapitulated in Scope and Significance of Paleo-ecology (1918). They have been consistently applied by Chaney and his associates with striking results in a noteworthy series of monographs on western fossil floras, particularly the Bridge Creek, Mascall, and Goshen (Chaney, 1925, 1933). As for the methods employed, the foremost is that of causal sequence, which involves the basic relation of habitat, plant, and animal, and which may be illustrated by the presence of *Stipa* in the Florissant Miocene. This suggests not only the existence of prairie but likewise of a grassland climate and a grazing population. A similar but even more fundamental sequence begins with deformation and finds successive expression in gradation, climate, and the biome of plants and animals, the latter regularly exhibiting the final effect. Both sequences are concerned in the method of community bonds in which the reactions and coactions of the component species in the complex organism are intimate enough to serve as the essential basis for reconstruction and interpretation. An important corollary of this is seen in the method of succession, especially in the form of the clisere or succession of climaxes in which climatic changes are at work. The essential feature of this is mass migration, with evolution, which yields the method of phylogeny.

An invaluable corollary of these is found in inference from distribution in space and in time. The latter enables us to close many a gap in the fossil record, and the former permits us to fill in the fragmented area of a dominant or community. This attains its most striking success in the form of the transad, and especially in that of the relict, where the community relation finds greater expression (Clements, 1934). Finally, an epitome of all other methods is that of cycles, in which it is recognized that all forces and effects exhibit cycles, not merely of deformation, erosion, and climate, but also of mass migration and evolution in the biome. Thus, evidence of elevation carries with it the necessary assumption of climatic shift as well as accelerated erosion, with inescapable effects in the climax series. Conversely, the displacement of a climax presupposes the chain of physical processes of which it is the final consequence. Out of all these principles springs the axiom that the present provides the surest route into the past and that reconstruction proceeds most reliably in that direction.

The former grassland climax.—The preliminary endeavor to outline the earlier grassland of the desert region was made a decade ago upon the basis of the relict grasses in the Colorado, Mohave, and Death Valley (Clements, 1922, 1923). As indicated previously, almost no perennial grasses survive today on the typical climax level and soil, except transient individuals ascribable to wet phases. Even though a product of the desert climate, the shrubby *Hilaria rigida* becomes dominant only in sandplains or washes, as is true likewise of the other most xeric species, *Triodia pulchella, Stipa speciosa,* and *Oryzopsis hymenoides.* In the driest part of the desert, where there is a rainfall of about 2 inches, such habitats supply compensation sufficient at least to double the rainfall in effect and to convert the climax of

Larrea-Franseria into a savannah of these with the grasses mentioned.

Toward the margins of the desert, where there is a rainfall of 5 inches, as in the vicinity of Goffs and Yucca, sand similarly increases the availability of the water content and supports a grass cover of *Hilaria, Sporobolus cryptandrus flexuosus, Muhlenbergia porteri,* and *Aristida purpurea.* With a corresponding rainfall in the desert generally, these constituted the chief vegetation, mixed or alternating with *Stipa* and *Oryzopsis* and dotted with taller *Larrea* and similar shrubs. Such a grassland was doubtless able to maintain at least a sparse population of camels, antelope, and horses, but bison were probably absent. Xeric forms of nearly all the species of rodents at present known for the region must have been present in abundance, and this presupposes a corresponding balance in carnivores.

Still proceeding backward, a further rise in precipitation to from 10 to 12 inches was marked by a prairie denser in texture and richer in species. In terms of the grazing animals, this was even more significant because of the presence of the grama-grasses of the genus *Bouteloua.* The evidence for this community is drawn from transads found in marginal areas as well as from mountain relicts, which are really transads in climatic terms. Thus, the relict prairie at 4300 feet in the Avawatz Mountains between the Mohave and Death Valley consists of *Poa scabrella* and *Hilaria jamesi,* in addition to the more xeric *Triodia, Oryzopsis, Stipa,* and *Aristida,* while at the northern edge on the slopes of the Argus Range occur *Hilaria jamesi, Poa scabrella,* and *Stipa comata.* In the district about Cabezon at the outermost edge of the Colorado Desert, a fine example of bunchgrass prairie persisted until it was plowed a few years ago. It was composed of *Stipa speciosa, coronata, setigera,* and *eminens, Poa scabrella,* *Elymus sitanion,* and *Koeleria cristata.* Even more eloquent are *Bouteloua gracilis* and *racemosa* in the neighboring mountains, and the unique relict east of San Diego at Jamacha, containing *B. hirsuta, radicosa,* and *rothrocki.* On the plateau that forms the eastern rim of the desert at Kingman, the desert plains consist of *Bouteloua eriopoda, B. gracilis, Aristida divaricata, A. purpurea, Sporobolus cryptandrus, S. c. flexuosus, S. strictus, Hilaria mutica,* and *Muhlenbergia porteri.* Still higher and to the east, at Seligman, where there is a rainfall of 15 inches, most of the species of the desert plains have yielded to the mixed prairie, comprising *B. gracilis* and *racemosa, Stipa pennata* and *comata, Sporobolus, Hilaria jamesi,* and others, with *Andropogon scoparius, furcatus* and, more rarely, *nutans* and *halli* in postclimax areas, such as valleys and sandhills.

Of the 25 species mentioned above, all but seven are transads and most, if not all, of those seven must have extended some distance into the region concerned. The consequence was a mixed prairie surpassing that of the present in wealth of species and in nutritive value as attested by eight short-grasses (six species of *Bouteloua, Hilaria cenchroides,* and probably *Buchloe dactyloides*) as well as by *H. jamesi,* which is outranked only by *B. gracilis* and *Buchloe* in food value. Naturally, not all the dominants grew intermingled, but the cover exhibited various groupings in accordance with the requirements of the species and the diversity of terrain. In the wet phases of the major climatic cycles, the animals must have reached not only the maximum in numbers, but also in size, as exemplified by the horses, camels, and elephants of the late Pliocene and early Pleistocene.

Among the grass transads are several tall-grasses such as *Andropogon saccharoides, A. glomeratus,* and *Imperata hookeri* that are subtropical in nature and derivation. A larger number of similar species occur westward into central Arizona, but stop short of the desert, namely, *Andropogon contortus, nutans, furcatus,* and *halli, Elionurus barbiculmis, Trachypogon secundus,* and *Tripsacum lemmoni.* All these find their best development in the southern part of the country and under a rainfall of 35 inches or more, though the first three range widely through the river valleys of the Great Plains, where they persist as relicts of an earlier warm-moist period. In their climatic relations in the United States they are typically postclimax to true prairie and subclimax to deciduous forest. This fact, taken with their occurrence from the South and East to the Canadian border and westward to Arizona or California, leaves little doubt that they constituted the dominants of an earlier tall-grass prairie that confronted the deciduous forests of the Eocene and Lower Oligocene and gradually replaced them as they withdrew in the face of cooler drier conditions in the later Oligocene and the Miocene. Their presence in the Southwest, both as transads and as adjacent dominants, justifies the assumption that they constituted the grassland that preceded the mixed climax described above and perhaps was still in occupation of much of the region before the Upper Oligocene.

The mid-grasses of the ancestral mixed prairie consisted of more xeric dominants, as the name suggests. These are all more northern in derivation and with lower water requirements than the tall-grasses. Some of them, such as *Stipa, Oryzopsis,* and *Hilaria,* were apparently North American in origin, while others were Eurasian. *Stipa* is the genus paramount of prairie and steppe the world over, and has probably played the major rôle not only in the evolution but also the intercontinental migration of grazing animals. Its indurated lemma, sharp callus, and long twice-bent hygroscopic awn stamp it as the product of a drying climate and give it distinct advantages over all its competitors in the processes of migration and ecesis. The genus is the final expression of the phyletic line of *Muhlenbergia-Oryzopsis-Stipa,* which is predominantly American and originally North American, the first genus having been derived apparently from *Calamagrostis,* primarily a meadow grass of high latitudes. The mid-grasses were evidently in process of dispossessing the tall-grasses after the deformation of the Upper Oligocene, as shown by fossil *Stipa* in the Miocene, and probably had reached the Southwest in Lower Miocene in time to play their part in the evolution of the Miocene grazing horses, *Merychippus* and *Protohippus.*

Further direct evidence of the presence of *Stipa* and its associates has been obtained by Elias from deposits of the Ogallala in the Lower Pliocene of western Kansas and adjacent Colorado (1932, 1934). In addition to several forms of *Stipa,* two other grasses occur, *Panicum* and *Berriochloa,* and four forbs of the borage family belonging to the genera *Biorbia* and *Krynitzkia.* It is an axiom that the evolution of a particular grassland must have preceded considerably the adaptation of the graminivorous animals to it, just as deformation and climatic change, or sometimes the latter alone, must have antedated the development or migration of a particular climax.

The short-grasses are likewise of American origin, but their homeland was the mountain plateaus of Mexico and Central America. Such far-ranging species as *Bouteloua gracilis* and *racemosa* and *Buchloe dactyloides* have pushed north to the Canadian border or beyond, but the majority are confined to the region west and south of Texas. *Aristida,* though of somewhat different form, is a regular associate of *Bouteloua* and of similar southern origin and xeric nature. The two genera constitute the chief dominants of the desert plains of today and hence the short-grasses of the Great Plains must have found their way into the mid-grass prairies of the Tertiary in a later dry period, perhaps as a result of Pliocene deformation. The short-grasses profit by overgrazing in competition with the taller species, and hence have spread irresistibly to the east during the historical period. They must have behaved similarly in some degree under the pressure of the great ungulate populations of the later Tertiary, in the evolution of which they apparently played a part. They "cure on the ground" and provide forage during the resting season that is far superior to that of the taller forms, their high nutritive value being associated with the unique starch-sheaths of the leaves. In contrast to the mid-grasses, they prospered under warmer drier phases of the climatic cycles, and at such times probably constituted the larger part of the forage.

The presence of a well-defined sagebrush climax lying above the grassland on slopes and plateaus, especially toward the north, is attested by the list of transads on page 98, which are dominants in this climax today. The most important of these are members of the main association typical of the Great Basin, but the coastal sagebrush of central and southern California is represented by several of the lesser dominants such as *Eriodictyum, Pentstemon,* and *Viguiera*. Two of the most important species, *Artemisia californica* and *Salvia apiana,* extend into the western edge of the Colorado Desert, while *Eriogonum fasciculatum* with its variety *polifolium* ranges across the desert and well to the east. No fossil remains of this climax have been found in or about the region, a fact readily explained by the general nature of the leaves and the arid habitat. As with the grassland, this community must have moved north and south and up and down the lower mountain slopes in its proper zonal relation in response to climatic pulsations and, as at present, it must have been the chief resource of the ungulates during periods of drouth.

The chaparral climax, representative of the next zone above with higher rainfall, naturally suffered more from the trend toward desiccation and the number of transads is correspondingly smaller. However, almost all the important genera except *Adenostoma* and *Heteromeles* are represented, mostly by species transads or by phylads that cross the desert, as in the case of *Quercus dumosa, Prunus demissa, Aesculus californica,* and *Cercis occidentalis.* Furthermore, an additional genus, *Garrya,* is found in the Pleistocene at Rancho La Brea; another, *Robinia,* in the Pliocene of the Ricardo; and a large number of the actual species occur in one or both of these horizons elsewhere in California. On the basis of phylogeny and association, chaparral must have been in existence in its proper position in the clisere of the Miocene or earlier, but it undoubtedly received recruits from time to time as the climate became drier. Although some of its dominants were undoubtedly utilized by browsers and the nuts and berries by rodents and birds, this community must have played a smaller part in the general economy.

In the existing vegetation, woodland takes a minor rôle as a climax, though in the reduced form of savannah it covers a wide area from the Edwards Plateau of Texas to the Coast Ranges and north into Oregon. Its major components are junipers, nut pines, and live oaks, though it may contain other pines and evergreens such as *Pinus sabiniana, Umbellularia,* or *Arbutus,* or, more rarely, such deciduous trees as *Quercus douglasi* and *Aesculus californica.* Probably the Joshua tree, *Yucca brevifolia,* finds its most natural position here also. As species with varieties, both *Pinus* and *Juniperus* were present, as was *Cupressus;* the evidence drawn from transads is confirmed by the occurrence of juniper and cypress at La Brea and Carpinteria and of cypress and nut pine at Ricardo. *Quercus agrifolia* is found in all three horizons, while *Q. douglasi* and *chrysolepis, Pinus sabiniana, Umbellularia, Arbutus,* and *Aesculus* occur in the Pliocene elsewhere in California, the last three extending at least as far back as the Miocene of the John Day region. In the form of phylads, all these except *Pinus sabiniana* occur across the desert today, and it is probable that in the Pliocene and wet phases of the Pleistocene the woodland was much the same as it now is about the Grand Canyon, in southern Arizona, and in a few relict areas in California.

As might be expected, the problem of the extent and composition of former forest in the desert region presents more difficulty. In the bordering ranges, especially, the frequent presence of *Pinus ponderosa, P. p. jeffreyi,* and *Pseudotsuga taxifolia* indicates that the montane forest was of wider occurrence before the Recent period, but its movement must have been chiefly if not entirely along mountain axes and not across the lowlands. The most plausible assumption is that climax mixed prairie had come into possession in the Lower Miocene and that this had been preceded by a tall-grass community in the beginning subclimax to hardwood forest, a condition visible today along the western border of the oak-hickory association. This border receives approximately 40 inches of rainfall at the present time, but it appears probable that more was needed in the Southwest to compensate for the evaporation caused by higher temperature and a longer season. In view of the fact that Chaney (1925:43) estimates the rainfall of the Mascall at 30 inches during Middle Miocene, a time when the oak-madroño forest was the chief community, it seems certain that it must then have been drier in the region of the present desert. This assumption is confirmed by the prevalence of *Merychippus,* and it seems fair to surmise that the precipitation amounted to about 20 inches and supported a grassland similar to but richer than that of central Nebraska today. This region is characterized along the valleys by relict forest, composed almost wholly of flood-plain species, such as willow, cottonwood, box elder, elm, ash, hackberry, and walnut, though bur oak and linden also reach it, and the more mesophytic oaks and hickories are not far to the east.

In attempting to explain the wide distribution of grassland and the associated ungulates in Miocene time, it is necessary to invoke land connections and to consider the great succession that followed the withdrawal of the Cretaceous Sea in the Laramie or Paleocene. The most satisfactory hypothesis is that the resulting marshes of vast extent were long peopled with reed-grass and sedge communities, as are the great tule swamps of California today, and that these for the most part yielded to tall-grass meadows in the Oligocene. With the broad connection between the two northern continents at this time, a wide pathway came into existence for the mutual exchange that took place in the Middle Miocene. Had this been limited to Holarctic forms, a mere change of climate might be sufficient explanation, but the movements of certain groups in opposite directions, such as those of the dogs, true cats, cattle, and elephants from Asia to North America and that of camels and horses from the latter to the former, presupposes an adequate connection at the north (Osborn, 1909; Matthew, 1915, 1930). The assumption of such an intercontinental grassland highway gains support from the great migration and expansion of *Stipa,* its associates, and the accompanying horses, tapirs, camels, and other forms in South America in the Pliocene and Pleistocene.

Fig. 1. *a*. Desert climax of *Larrea-Franseria,* the leaves killed by the 1934 drouth phase of the climatic cycle.

Fig. 1. *b*. *Larrea* transad relict in the grassland of the upper San Joaquin Valley.

Fig. 2. *a*. Postclimax *Hilaria rigida* in a sandy wash, central Mohave Desert.

Fig. 2. *b*. Relict *Stipa* and *Aristida* among the blocks of a lava ridge, Death Valley.

Fig. 3. *a. Stipa speciosa, Oryzopsis,* and *Poa* in an open savannah of *Yucca-Larrea* in Antelope Valley, the western arm of the Mohave Desert.

Fig. 3. *b. Stipa* prairie between Banning and Cabezon at the western edge of the Colorado Desert.

Fig. 4. *a*. Reed-swamp associes of *Scirpus, Juncus,* and *Phragmites,* Death Valley.

Fig. 4. *b*. Open woodland of Joshua tree (*Yucca brevifolia*), western Mohave Desert.

Fig. 5. *a. Washingtonia filifera* in canyons of the foothills near Indio, Colorado Desert.

Fig. 5. *b. Parkinsonia torreyana* in valleys of the dune-complex, Algodones, Colorado Desert.

Fig. 6. *a.* Consociation of *Elymus triticoides* in the McKittrick region, upper San Joaquin Valley.

Fig. 6. *b.* Postclimax tall-grass, *Andropogon saccharoides*, in a trackway depression, Gila Desert, Arizona.

Fig. 7. *a.* Desert-plains association with *Yucca* and *Ephedra* in southwestern New Mexico.

Fig. 7. *b.* Mixed-prairie association near Seligman in northern Arizona.

There is almost no direct fossil evidence of the nature and composition of the deciduous forest in the desert region during the Tertiary. The nearest plant deposits of the Miocene are those of Esmeralda in Nevada and Table Mountain in the central Sierra, neither of them adequate to the purpose. The most satisfactory flora is that of the Mascall (Chaney, 1925; cf. also Berry, 1929); however, for the most part this lies 7 or 8 degrees to the north and the species must have been much changed or reduced so far to the south. The fauna of the Mascall is thought by Merriam and Sinclair (1907) to denote open forest and savannah, while that of the Barstow indicates an open well-grassed country (Merriam, 1919:450). The presence of *Quercus agrifolia* in the Pleistocene of La Brea and the Pliocene of Ricardo is suggestive only of savannah such as occurs today through the southern half of cismontane California.

The conclusions to be drawn from transads are more satisfactory in respect to the nature and composition of the forest, but are less clear in respect to time. The transads of *Juglans, Acer, Platanus,* and *Fraxinus* indicate the probability that these were associated with the existing willows and cottonwoods as late as the wet phases of the Pleistocene and through most of the Pliocene. However, with the aid of indices drawn from adjacent fossil floras, regional faunas, and from climatic correlations, it is possible to reconstruct climaxes and postclimaxes that may serve as useful working hypotheses. During the wetter portions of the glacial period, there was probably woodland along the valleys, on broken ridges, and in sandy tracts, composed of *Quercus agrifolia, dumosa, douglasi,* and *Arbutus, Aesculus,* and *Prunus,* but the evidence of grazing animals suggests that these did not form a climax even as early as the Miocene. This view is confirmed by the Mascall, which grew in a cooler, more humid climate.

To obtain a glimpse of the hardwood climax that covered the region before this time, it is desirable to turn to the outposts or, better, the rear guards of the great deciduous forest of the East as they exist today. Of the dominants of the three associations, only a few fail to reach eastern Nebraska and Kansas on the north and Texas on the south, and most of them belong to the more eastern oak-chestnut community, namely, *Castanea dentata, Quercus prinus,* and *Liriodendron.* By contrast, 25 are found today at the edge of the oak-chestnut association and some of these extend well beyond it in relict areas. In this list are *Acer saccharum* and *Fagus americana,* 10 species of *Quercus,* 6 of *Hicoria,* 2 of *Tilia,* and one each of *Magnolia, Persea, Prunus, Aesculus,* and *Nyssa.* The sugar maple still persists in the cool recesses of Caddo Canyon in central Oklahoma, *Quercus texana* and *acuminata* linger in the mountain ranges of western Texas, *minor* grows as a shrub in the sandy plains of the Panhandle region, *macrocarpa* survives around the Black Hills as well as in northeastern Wyoming, and *Liquidambar* occurs south of Texas to the highlands of Guatemala.

Among the important subdominants of layers or margins, nearly all are to be found from eastern Nebraska to Texas, namely, *Carpinus, Ostrya, Asimina, Cornus, Diospyrus, Morus, Sassafras, Ilex, Rhamnus, Maclura, Crataegus,* and *Malus. Carpinus caroliniana* persists as a relict in the mountains of southern Mexico and Central America; *Ostrya virginiana* is represented by a single outpost, *O. knowltoni,* at the Grand Canyon; *Morus celtidifolia* occurs in southern New Mexico and Arizona, stretching southward in the mountains from Mexico to Peru; and *Ulmus* reaches northwest Nebraska as the species *thomasi* and western Texas as *crassifolia.* Such important seral dominants as *Ulmus, Celtis,* and *Fraxinus* follow the rule in persisting far westward along river valleys; *U. americana* reaches the Black Hills and Rocky Mountains, and *fulva,* western Kansas; *Celtis occidentalis* attains western Washington in the north, and several species of willow are found westward to the Pacific Slope.

It is hardly necessary to emphasize the fact that climax relicts west of the deciduous border have survived because of edaphic compensation in terms of stream valleys, altitude, slope-exposure, or soil and that, in consequence, they indicate water relations higher than that of the circumjacent climax but lower than that of their own climax to the east. Such species, in conjunction with seral dominants, permit the plausible reconstruction of a postclimax along streams not much different from that of the Niobrara, Platte, and Republican in Nebraska and of the rivers of central Texas today. The rainfall of the enclosing prairie climax fluctuates about 25 inches in the north and 30 in the south, the effective values being much the same as a result of the evaporation gradient.

In considering as indexes the dominants that still confront the prairie climax, it is significant that three-fourths of them find their western limit in one of the three parallel valleys of central Texas, the Trinity, Brazos, and Colorado, while at the north the majority still persist in the valley of the Missouri along southern Nebraska and adjacent Kansas. This belt falls for the most part between the isohyets of 30 and 40 inches with that of 35 as the median line; however, the full climax of oak-hickory finds its boundary at approximately 40 inches. If this relation be applied to the region of the present desert, it leads to the conclusion that such a forest was in complete or major occupation at a rainfall of this amount, and that it had already withdrawn to valleys and other compensatory sites when the precipitation had dropped to 35 inches. On the basis of Chaney's conclusions for the Bridge Creek of the John Day region (1925), which is in much the same longitude, the hardwood climax might well be referred to the same period, the Upper Oligocene. But the desert region lies several hundred miles south of the regular storm track, and hence should have been distinctly drier as well as somewhat warmer than central Oregon. This suggests the Lower Oligocene or Upper Eocene as the more probable time, an assumption that draws support from the similar composition of the much earlier hardwood forests of the Dakota Cretaceous, as well as the later Fort Union, in which occur practically all the generic dominants of the modern deciduous climax.

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The Strand and Dune Flora of the Pacific Coast of North America: A Geographic Study

By William S. Cooper

PREFACE

Fifteen years ago I undertook a comprehensive investigation of the sand dunes of the Pacific coast of North America, in which physiography and vegetation were to have an equal share of attention. The field work has been brought to practical completion, and this paper embodies the first published results of the study.

The body of data which forms the basis of the present essay rests primarily on my own observations—on lists and collections made in the course of repeated visits to southeastern Alaska and to all important dune areas from Puget Sound to northern Baja California. In addition, I have personally examined the specimens of the plants concerned deposited in the following herbaria:

University of Washington
University of California
California Academy of Sciences
Leland Stanford Jr. University
Pomona College
Missouri Botanical Garden
University of Minnesota
Field Museum of Natural History
United States National Herbarium
New York Botanical Garden
Gray Herbarium

I wish to express my appreciation of the courtesies extended to me by those in charge of these herbaria, and particularly for additional data supplied by letter. The literature has also been explored as thoroughly as possible. The ranges plotted on the maps are based upon all these sources. Records founded on doubtful specimens and uncertain references have been rigorously excluded.

Valuable information has come to me through correspondence with Dr. R. F. Griggs, of George Washington University; Dr. Eric Hultén, of Lund, Sweden; Miss Isobel W. Hutchison, of Carlowrie, Kirkliston, Scotland; Dr. W. L. Jepson, of the University of California; Dr. W. L. G. Joerg, of the American Geographical Society; Dr. H. M. Raup, of the Arnold Arboretum of Harvard University; and Dr. Vilhjalmur Stefansson, of New York City.

Compilation of data has been done under my direction by Miss Faith P. Hall, Miss Dorothea Fritz, and Mr. Frank E. Egler. Mr. Egler prepared most of the maps. It is a pleasure to acknowledge financial assistance given to me by the Graduate School of the University of Minnesota.

GENERAL SURVEY

The coastal province which constitutes the field of this study extends from southeastern Alaska to Socorro, Baja California. The southern limit merely marks the end of the territory that I have personally explored. There are no adequate data for extending the survey farther. Within this province, consideration has been strictly confined to the flora of the strand and dunes.

Without attempting a detailed ecologic analysis, we may divide the vegetation of these habitats into two communities, which will serve equally well as units for floristic study. One community inhabits the actual strand or upper beach and the areas of moving and accumulating sand, particularly the foredunes; the other occupies the surfaces of stabilized dunes.

The first is distinctively maritime and will receive the larger share of our attention. Selection of species is an easy matter because the habitat is narrowly circumscribed and very definite. Only native species are considered. Two important plants native elsewhere have recently become established. *Cakile edentula* (Bigel.) Hook. has appeared spontaneously, is widely distributed, and behaves like a native. A map giving its present distribution is provided (fig. 6*b*). *Ammophila arenaria* (L.) Link, planted as a sand-binder in many places, promises to make itself thoroughly at home.

The flora of the stable dunes is much less definite, and selection of a representative list is consequently more difficult. Within the glaciated region there are scarcely any areas of stabilized sand. In Washington and Oregon, such areas are occupied by shrubs and forest trees having no relation to strictly maritime conditions.

In central and southern California there is a definite community which occupies dune surfaces as fast as sand movement comes to an end, and which is superseded by chaparral, the climax. This community consists of several short-lived shrubs as dominants and an extensive list of subordinate herbs. A large part of these are strictly coastal, rarely straying from the dunes; others, although most characteristically dune species, also occur to some extent in other environments and range inland for varying distances. These two classes are included in the present study. A third group is made up of species not characteristically coastal, but of considerable importance on stabilized sand. Prominent among these are certain members of the "coastal sagebrush" community of southern California, especially *Eriogonum fasciculatum* Benth., *Salvia mellifera* Greene, and *Artemisia californica* Less. Because of the common presence of these and their similarity in ecologic make-up, this "dune shrub" community may fairly be considered a minor unit within the coastal sagebrush. In selecting the list for floristic study, an effort has been made to include only those species that are characteristically coastal. Naturally there is abundant opportunity here for difference of opinion.

In Baja California the coastal sagebrush type is replaced by another shrub community with desert affinities. Our knowledge of it is too limited to warrant its consideration.

The concept of the species here adopted is a broad one. Acceptance of the larger unit as fundamental, with full recognition of the smaller units contained within it, seems the most useful procedure in floristic study. Of the genus, also, the concept is usually a broad one, and for the same reason. It has seemed necessary to replace some long-familiar names with unfamiliar ones; when this is done, the better-known name is added in brackets.

RANGES OF SPECIES

Species of Strand and Shifting Dunes

Poa.—Three species of *Poa,* probably related, are characteristic dune plants on the northern Pacific coast of the United States. Mutually equivalent ecologically, they are found usually on feebly moving sand in relatively sheltered places not in immediate proximity to the shore. *Poa confinis* Vasey (fig. 1*a*) goes farthest north (Comox, east side of Vancouver Island) and extends southward to Mendocino County, California (Inglenook). It is extensively overlapped by *P. macrantha* Vasey (fig. 1*c*), which goes not so far north (Whidbey Island, Puget Sound), but a little farther south (Point Arena, Calif.). *P. douglasii* Nees (fig. 1*b*) overlaps the first two in northern California; it begins at Point St. George, Del Norte County, and extends farther southward than the others to Point Sur, Monterey County.

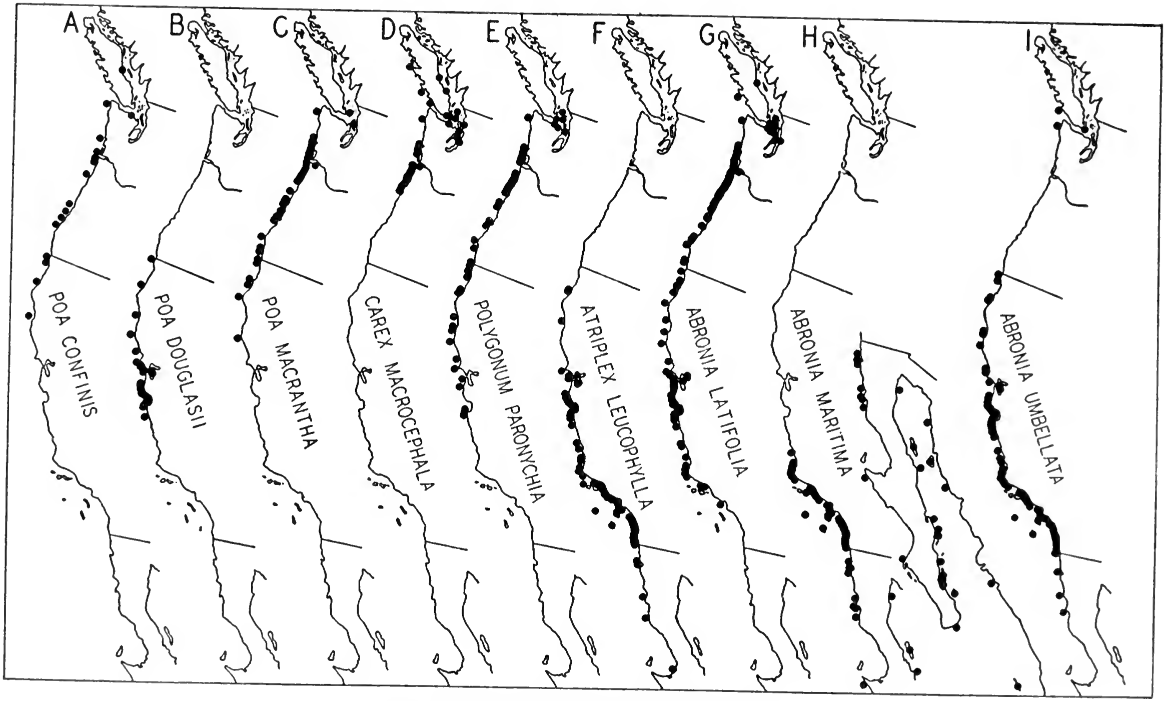

Fig. 1. Species of strand and shifting dunes.

Poa macrantha is related to *P. eminens* Presl, a coastal species of northeastern Asia and arctic America (Hultén, 1927–30), and to *P. labradorica* Steudel of the coast of Labrador. It may perhaps have become differentiated in the course of migration of subarctic stock southward along the Pacific coast. *Poa confinis* and *P. douglasii* are probably close relatives, but their affinities with other species are not clear. It is at least a reasonable hypothesis that they originated in the same way.

Elymus arenarius L. var. *villosus* E. Mey. (figs. 2*a*, 3*a*) is the most characteristic and conspicuous strand-plant on the shores of the northern Pacific ocean. In southern Alaska it forms a belt of nearly pure growth at the top of the beach. South of Puget Sound, it inhabits the foredune zone and forms small hillocks. Southward it becomes progressively less abundant. Its southern limit in 1927 was very definitely fixed at the mouth of the Salinas River on Monterey Bay.

This species, in its two principal varieties, is probably circumpolar in distribution. The typical form inhabits the northwestern coasts of Europe—the British Isles, the southern Baltic, Norway, Iceland. The variety *villosus* E. Mey. [subsp. *mollis* (Trin.) Hultén] occurs on the coasts of northeastern America southward to Cape Cod (St. John, 1915), Hudson Bay, the Arctic Archipelago, the entire coast of Alaska, and southward on the Pacific coast of America as outlined above. It continues along the Aleutian Islands to the coasts of eastern Siberia, Kamchatka, Manchuria, and Japan. Reported occurrences at the mouth of the Lena River and the Taimyr Peninsula indicate that its range is probably fairly continuous along the arctic coast of Siberia, thus connecting with that of the typical form. The species occurs also on the shores of large interior lakes—Ladoga and Onega in Russia; Superior, Michigan, Athabaska, and probably others in

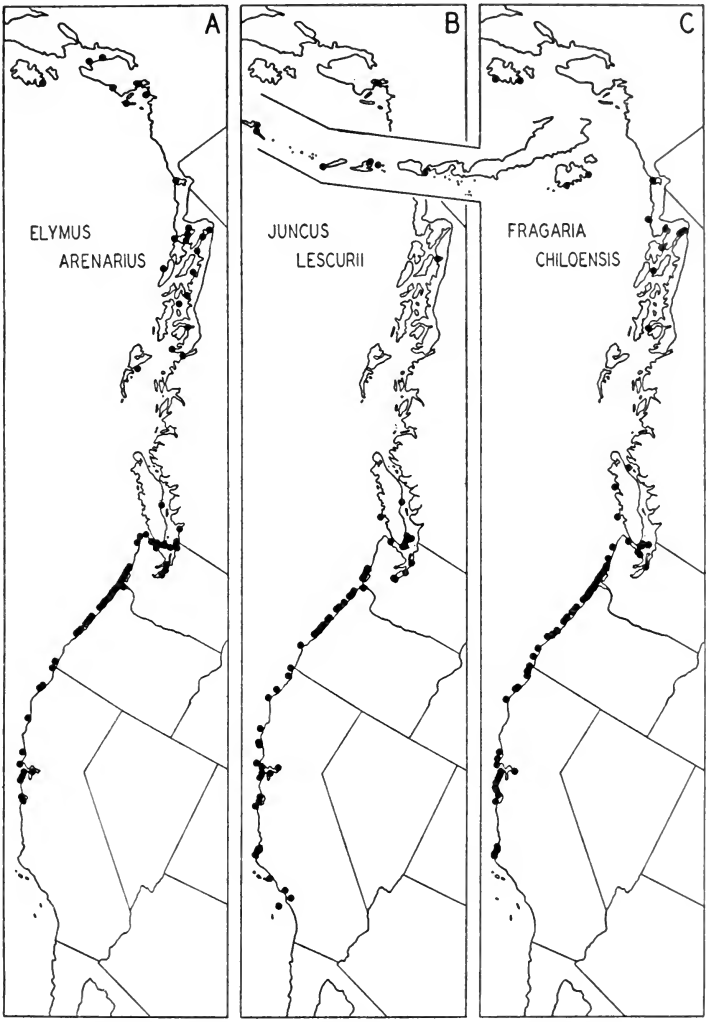

Fig. 2. Northerly-ranging species of strand and shifting dunes.

North America. A form transitional between the type and var. *villosus* occurs in Greenland.

Carex macrocephala Willd. (including *C. anthericoides* Presl) (figs. 1*d*, 7) grows close to the strand and is capable of forming small dunes. It occurs on both the American and the Asiatic coasts of the northern Pacific Ocean. On the American side, its southernmost recorded occurrence is at De Lake, Lincoln County, Oregon. It is abundant in northern Oregon and southern Washington, and frequently is found in northern Washington, the Puget Sound region, and on both coasts of Vancouver Island. North of there, it has been reported from a few scattered localities—Sitka, Yakutat Bay, Cook Inlet, and Kodiak Island. On the Pacific coast of Asia it reappears in Kamchatka, and there are frequent records of its occurrence southward along the islands and mainland coast to southern Japan and middle China.

Fernald (1930) treats the Asiatic and American forms as distinct species, accepting the name *C. anthericoides* Presl as applicable to the latter. Mackenzie (1931) prefers, in the present state of our knowledge, to regard them as one. According to Fernald, the Asiatic *C. macrocephala* has become established on the coast of New Jersey, where it is spreading rapidly. *Carex macrocephala* has no close relatives and is the only species in its section.

Juncus lescurii Bol. (fig. 2*b*) is included in this list with some hesitation, because it is not necessarily associated with moving sand. Its typical habitat is the wet sand of "pannes," areas in the dune complex which have been eroded by wind to the vicinity of the water table. When these are invaded by freshly blowing sand, *Juncus* becomes an effective dune builder.

The authentic range of the species follows the coast from Vancouver Island southward to Los Angeles County, California. It makes a few scattered appearances north of Vancouver Island, the farthest being at Prince William Sound, Alaska. It is reported from a number of places in the interior of California, Oregon, and Washington, and even in Idaho. The specimens from these regions that I have seen are consistently very different in aspect from the coastal form, and seem to agree with the description of *J. textilis* Buch. (*J. lescurii* var. *elatus* Engelm.).

The species occurs also on the Pacific coast of South America. It is reported from Ecuador, Chile, Argentina, Patagonia (Buchenau, 1906; Skottsberg, 1910, 1916). According to Buchenau, it is a good species, but transitional forms occur with *J. balticus* Willd., which is found in Europe, North and South America, and Asia, and with *J. andicola* Hook., an inhabitant of the Andes from Colombia to northern Chile.

Polygonum paronychia C. and S. (fig. 1*e*) is a minor but common inhabitant of unstable sands, usually not close to the strand. Its range is not extensive—from Puget Sound on the north to Monterey Bay on the south. It belongs to the section *Avicularia,* which includes several species partial to sea beaches.

Atriplex leucophylla (Moq.) Dietr. (fig. 1*f*), most aggressive of the foredune builders in its advance toward the sea, is confined to the coast of California and Baja California, ranging from Humboldt Bay on the north to Bahía de Sebastián Vizcaino on the south. It occurs also on the islands off the coast of southern California. It seems to belong with the *pentandra* group of the subgenus *Obione,* but is more primitive than the species which seem nearest to it (Hall and Clements, 1923). It is one of the least variable of the North American species. According to Hall and Clements, it seems probable that it originated in Mexico and became separated from the ancestral line in the course of its northward migration.

The genus *Atriplex* is preëminently characteristic of saline habitats—sea strands, and steppes and deserts with salt-impregnated soils (Volkens, 1893). Throughout the temperate and subtropical regions of the earth, wherever such an environment is found, species of *Atriplex* form an important element in the vegetation. The great majority of the North American members are inhabitants of the semidesert regions of the Southwest. Several species of southern California, Baja California, and the Mexican mainland are rather closely restricted to the strand.

Abronia.—Two species of this genus are important members of the foredune community; a third is common but of lesser ecologic significance. *A. latifolia* Eschsch. (fig. 1*g*), one of the most important foredune builders, ranges from Vancouver Island (Comox and Ucleulet) southward to Santa Monica in southern California. *A. maritima* Nutt. (fig. 1*h*) has a more southern range, from Morro, San Luis Obispo County, California, to the tip of Baja California, and on the Mexican coast to Tepic at least. *A. umbellata* Lam. (fig. 1*i*) is a variable species, or a species-complex, of little importance as a builder of hillocks. Standley (1918) recognizes five forms as specifically distinct. *A. acutalata* Standley, found in a few localities in the Puget Sound region, is entirely isolated from the others. *A. breviflora* Standley inhabits the coast of Del Norte, Humboldt, and Mendocino counties, California. Typical *A. umbellata* ranges from Marin County, California, to southern California. *A. alba* Eastw. and *A. minor* Standley are found on the coast of southern California, and the former also on the islands off the coast. A sixth form, *A. gracilis* Benth., rather more distinct than the others, occurs from southern San Diego County to Magdalena Bay, Baja California.

Abronia is a North American genus, occurring chiefly in the western United States. One or two species extend into southwestern Canada and three or four into northern Mexico (Standley, 1909). Standley (1918) recognizes 28 species. Among these *A. latifolia* and *A. maritima* stand out as distinct units. The group *Umbellatae* includes the coastal species listed above and four interior species. These latter and the remaining members of the genus are almost without exception inhabitants of desert and semidesert regions. Standley remarks (1909): "Most if not all the species seem to be in a variable or mutating state. They are rather numerous and most of them are confined to comparatively small areas."

Honckenya peploides (L.) Ehrh. [*Arenaria peploides* L.; *Ammodenia peploides* (L.) Rupr.], figures 3*b*, 4*a*, is strictly a strand plant. It is closely associated with *Elymus arenarius,* but for the most part prefers the open beach outside the heavy growth of the grass. On the Pacific coast of North America its range extends from Alaska southward to Oregon (Coos Bay).

The species is probably circumpolar, and its distribution is closely similar to that of *Elymus*. It inhabits the coasts of northwestern Europe, Nova Zembla, Spitzbergen, Iceland, Greenland, the American Arctic Archipelago, the entire coast of Alaska, and the Aleutian Islands. In arctic Siberia it is reported from the mouth of the Yenisei River (Hultén, 1927–30), and may occur generally along that coast ("arctic Siberia": Holm, 1922). It is common on the Atlantic coast of North America southward to Cape Henry, Virginia, and on the Pacific coast of Asia to Korea and Japan.

Several varieties have been described, the most important being var. *diffusa* Hornem., Greenland and arctic America; var. *robusta* Fernald, Atlantic coast of North America from Quebec to Virginia; and var. *major* Hook., coasts of the northern Pacific Ocean (Fernald, 1909; Hultén, 1927–30).

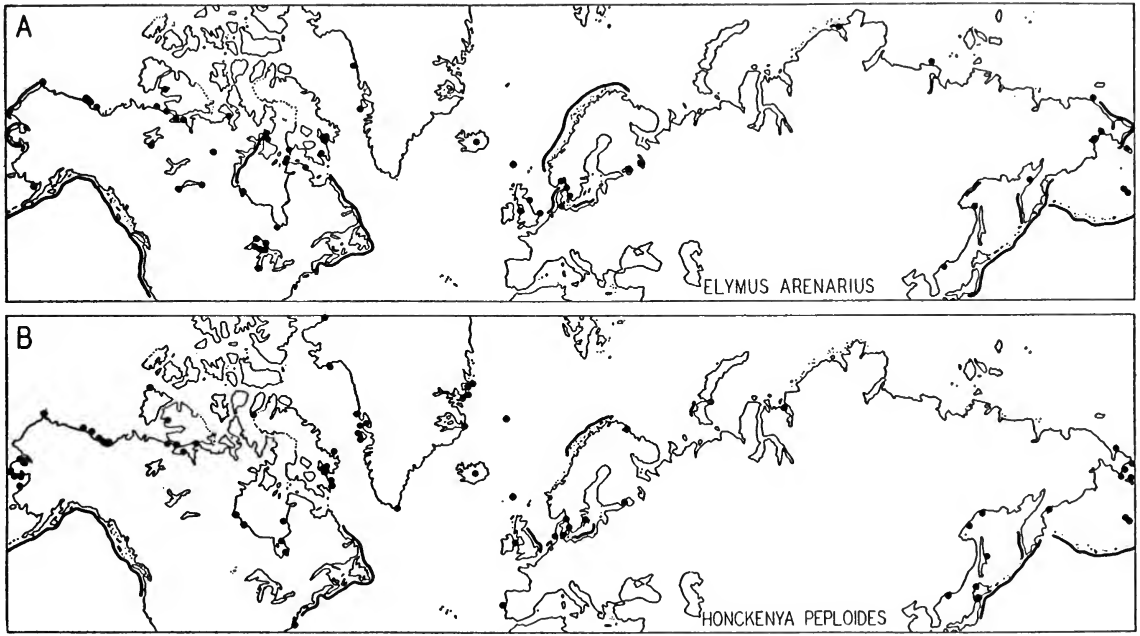

Fig. 3. Species of subarctic distribution.

Carpobrotus chilensis (Molina) N. E. Br. [*Mesembryanthemum aequilaterale* Brewer and Watson], figure 6*a*, an extreme succulent, is a very important member of the foredune community. It is not especially noteworthy as a mound former, but is effective in binding the surface of hillocks initiated by other species. The known range on the Pacific coast of North America extends from Cape Blanco, southern Oregon, southward to Socorro, Baja California; it is quite possible that it may occur farther in that direction. It is most abundant on the coast of California from San Francisco Bay to the Mexican boundary. It also is found on the coast of Chile.

The genus *Mesembryanthemum* as treated by earlier authors is a group of enormous size, mainly confined to South Africa. Its members are more or less succulent, most of them very decidedly so. N. E. Brown has pointed out the fundamental diversity existing within the group and has accordingly made division into numerous genera.

The plant of the Pacific coasts of North and South America has been assigned to the genus *Carpobrotus* (Brown, 1925), a group of from 15 to 20 species, two-thirds of which are confined to South Africa. The four recognized Australasian species were formerly combined with the American plant as *Mesembryanthemum aequilaterale. Carpobrotus* is the most widely distributed genus of the entire group (Brown, 1928). It also is reasonable to assume that it is closest to the primitive stock because, with its elongated stems and numerous leaves, it is not far removed from the norm of plant habit. In the course of migration from its African home to Australasia and America, it has become differentiated into several species not notably divergent from the type. In the meantime the stay-at-home contingent has indulged in a wild orgy of evolutionary development, in which practical elimination of stem and reduction of leaf surface to the minimum have been the dominating tendencies.

Fragaria chiloensis (L.) Duch. (fig. 2*c*), on the coast of Washington, Oregon, and California, is a minor species of the foredune zone. Its rôle is to bind the surface rather than to form hillocks. In Alaska it grows upon the strand, mingling with *Elymus* and *Lathyrus,* and in the tundra-like community that often lies adjacent. It ranges from Atka Island in the Aleutian chain southward to Santa Maria, California. It is not reported from the coast of Mexico and Central America, but occurs along the western side of South America from Ecuador to Patagonia. Here it is not exclusively coastal. Skottsberg (1910, 1916) states that it is found in steppe and meadow-like communities and inhabits gravelly river banks. Donat (1931) speaks of its occurrence in forests of *Nothofagus pumilio.* It is recorded from a number of localities on the eastern slopes of the southern Andes and from one point on the Atlantic coast of southern Argentina. One specimen is labeled "Bolivia." It occurs also on Juan Fernandez, and on the Hawaiian Islands in the mountains at elevations of from 4500 to 10,000 feet.

Lupinus littoralis Dougl. (fig. 6*c*) is a species of little ecologic importance. It inhabits feebly moving sand away from the shore, usually in company with *Poa macrantha.* It ranges from Comox, on the eastern shore of Vancouver Island, southward to Point Reyes, California. A closely related species, *L. tidestromii* Greene, is found in similar habitats on the Monterey Peninsula and at Point Reyes.

Lathyrus.—Two species of this genus occur on the Pacific shores of North America. One ranges widely in north temperate and subarctic regions; the other is endemic. *Lathyrus japonicus* Willd. [*L. maritimus* (L.) Bigel.], figures 4*b,* 5*a,* is strictly a

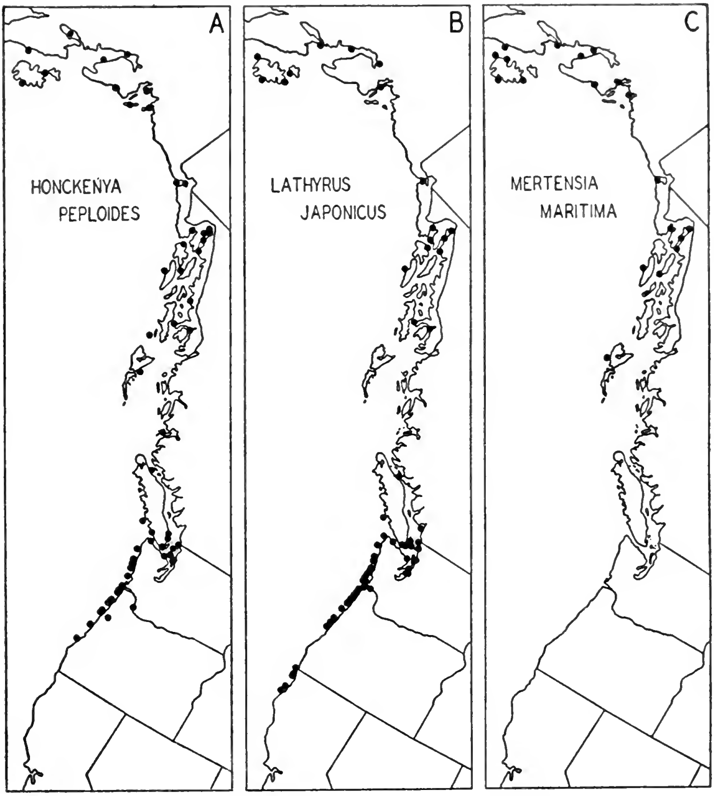

Fig. 4. Northerly-ranging species of strand and shifting dunes.

strand species, growing on the beach with *Honckenya* and *Elymus*. Its range extends from Alaska southward to northern California (Humboldt Bay). In general distribution it is very similar to its companion species, *Elymus arenarius* and *Honckenya peploides,* but is somewhat more restricted. It is common on the shores of the Baltic, the coasts of the British Isles and Norway, the Arctic coast of Russia, in Iceland, and extreme southern

Greenland. In North America it ranges from Labrador southward to New Jersey and is found on the eastern shores of Hudson Bay. It is not recorded from the Canadian Arctic Archipelago, but reappears at Shingle Point, near the mouth of the Mackenzie River (Macoun and Holm, 1921). There are no records of its occurrence on the northern coast of Alaska. It is common on the southern and western coasts of Alaska, on the Aleutian Islands, the coasts of eastern Siberia, and Kamchatka, and ranges southward to Korea and Japan. There are no records of it from the arctic coast of Siberia. Like *Elymus,* it grows on the shores of large lakes in Russia and North America. Its most striking difference in distribution from *Elymus* and *Honckenya* is its practical absence from the arctic coasts of America and Asia. It is found on the coast of southern Chile from S Lat. 41° to S Lat. 47° (Reiche, 1896, 1907; Macloskie, 1903–06).

Fernald (1932) has noted the unfortunate necessity of abandoning the familiar name *Lathyrus maritimus* in favor of *L. japonicus.* In the same paper he distinguishes four varieties and remarks as follows with regard to the history of the species (p. 187):

> Phylogenetically *Lathyrus japonicus,* var. *aleuticus,* occurring as a tolerably uniform plant around the arctic and subarctic areas, would seem to be the primitive or ancestral type, which, pushing southward into more temperate conditions, has become modified into the glabrous but thin-leaved *L. japonicus* var. *typicus* and into the two coarser and heavier-leaved extremes of temperate regions, vars. *glaber* and *pellitus.*

Lathyrus littoralis (Nutt.) Endl. (fig. 6*d*) is a minor species of the foredunes, not equivalent to *L. japonicus* in ecologic rôle. It ranges from Vancouver Island (Ucleulet) southward to Monterey Bay, California.

Oenothera cheiranthifolia Hornem. (fig. 6*e*) is frequent in partly stabilized sand away from the immediate shore. Its range extends from central Oregon (Coos Bay) southward to Socorro, Baja California. Two forms superficially very different are combined by Munz (1928) under the specific name here accepted. These are *O. cheiranthifolia* var. *typica,* ranging from Oregon to southern California, and *O. cheiranthifolia* var. *suffruticosa* S. Wats. [*O. viridescens* Hook.], Point Conception to northern Baja California.

The family *Onagraceae* is mainly American, and the complex genus *Oenothera* especially so. The subgenus *Sphaerostigma* (often segregated as a genus) includes, according to Munz, fourteen species occurring in North America. The genus is present also in South America, and several of the North American species may occur there also. The North American members, aside from *O. cheiranthifolia,* are inhabitants of desert and semidesert regions. Three of these (*O. contorta* Dougl., *O. hirta* Link, and *O. bistorta* Nutt.) have coastal varieties.

Glehnia littoralis Schmidt [*Cymopterus littoralis* Gray] (figs. 6*f*, 7), inhabits the northern Pacific shores of both America and Asia. The two populations are regarded as specifically distinct by Miss Mathias (1928); the American form assumes the name *G. leiocarpa* Mathias. This form is common from Puget Sound to Point Arena, California. North of Puget Sound the only record is from Yakutat Bay, Alaska. *G. littoralis,* treated as distinct, inhabits the coasts of Manchuria and China, Saghalin, the Kurile Islands, and Japan. It is not present in Kamchatka nor on the other portions of the Siberian coast.

For this species we are fortunate in possessing a fossil record. Fruits certainly referable to *Glehnia* have been found in Pleistocene asphalt deposits at Carpinteria, California, more than 400 miles beyond the present southern limit of the species (Chaney and Mason, 1933).

A number of genera including *Glehnia,* formerly combined under *Cymopterus,* have their homes almost exclusively in western North America. Their united ranges extend from western Missouri to the Pacific Coast and from southern Canada to northern Mexico (Mathias, 1930). *Glehnia* is the only one that transgresses the boundaries of this region.

Convolvulus soldanella L. (fig. 6*g*) is an important species of the foredune zone; it binds surfaces effectively but does not form hillocks. Its range on the Pacific coast of North America is from Vancouver Island (Ucleulet) southward to the Mexican boundary and perhaps beyond. This species has by far the widest distribution of our entire list; it is found upon the coasts of all the continents except Africa. It occurs in western Europe upon the British Isles, the mainland shore of the North Sea, the Atlantic coast of France, and in the northwestern part of the Mediterranean; in Japan, Manchuria, China, the East Indies, Australia, and New Zealand; and on both coasts of southern South America.

The *Convolvulaceae* as a whole are a tropical family and are especially well developed in Asia and America. *Convolvulus soldanella* represents a genus that is not typically coastal, but well distributed over the temperate and subtropical parts of all continents (Peter, 1897).

Mertensia maritima (L.) G. Don (figs. 4*c,* 5*b*) is strictly a strand plant, almost exactly equivalent to *Honckenya peploides* in habitat preference. In southward extension along the Pacific coast of North America it is the most restricted of the group of northern littoral species. Its known range ends at the Queen Charlotte Islands. In general distribution it is very similar to its

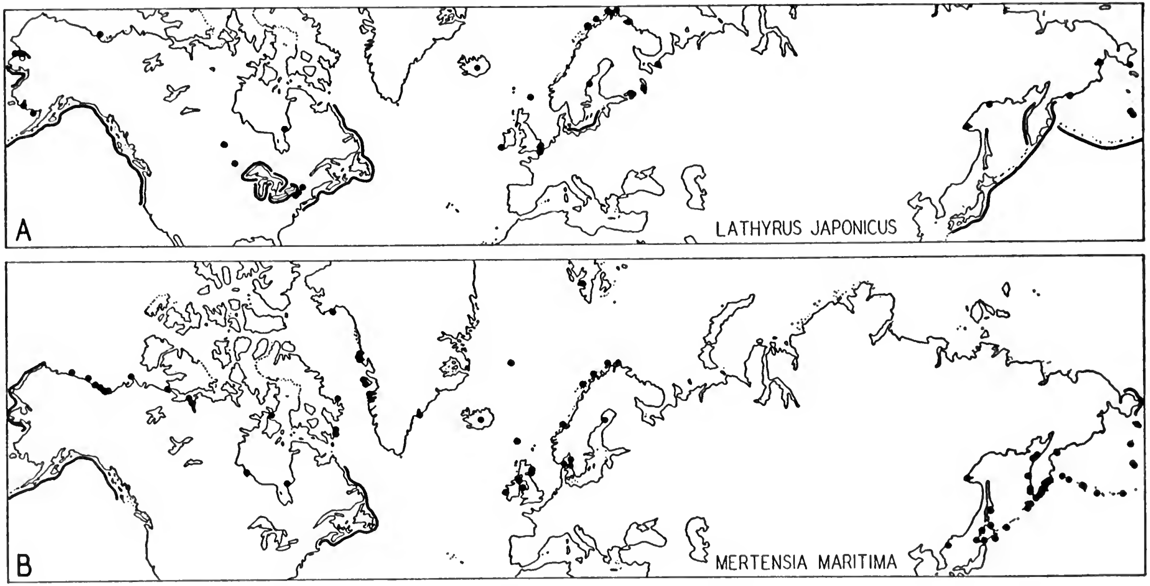

Fig. 5. Species of subarctic distribution.

three companion species. It is found on the coasts of arctic Russia and Norway, in the British Isles, in Denmark, Spitzbergen, Jan Meyen Island, Iceland, and Greenland. On the Atlantic coast of North America it ranges southward to Nantucket Island. It is found on the shores of Hudson Bay, in the Canadian Arctic Archipelago, on all coasts of Alaska, the Aleutian Islands, eastern Siberia, Kamchatka, and southward in Korea and Japan. There seem to be no records of its occurrence on the arctic coast of Siberia, except in the vicinity of Bering Strait. The Asiatic form has been distinguished as subsp. *asiatica* Takedo (Hultén, 1927–30). MacBride (1916) gives this form specific rank.

The genus *Mertensia* is found in the north temperate regions of the Old and the New World (Gürke, 1897). Extensive development of the genus in the mountain regions of western North America may be a relatively recent event in its history. There seems to be no genetic connection between this group and *M. maritima.*

Franseria bipinnatifida Nutt. (fig. 6*h*) and *F. chamissonis* Less. (fig. 6*i*), ecological equivalents, are conspicuous members of the foredune community. They commonly produce low mounds, but are not particularly efficient in this because they lack capacity for upward elongation. They are far more important as secondary invaders of hillocks already established by other species.

Of the two, *F. bipinnatifida* has the more extended range. The northernmost certain locality is Ucleulet, Vancouver Island. It has been reported from Nootka Sound, Vancouver Island (Macoun, 1883–90), and from Queen Charlotte Islands (Macoun, *loc. cit.,* on authority of Dawson), but these records need verification. The southernmost localities in North America are

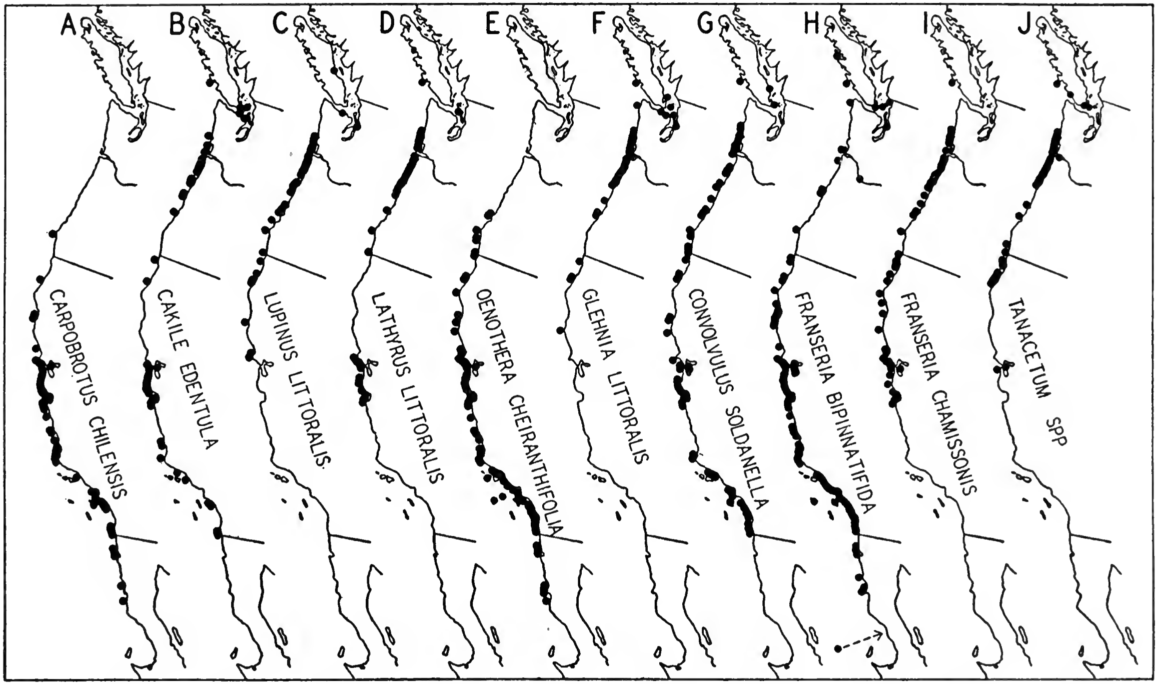

Fig. 6. Species of strand and shifting dunes.

Guadalupe Island, off the coast of Baja California, N Lat. 29°, and, on the peninsula, San Ramón, N Lat. 32°. Very likely it goes farther south. *F. chamissonis* has a much less extended range—from Ucleulet, Vancouver Island, on the north, to Monterey Bay on the south.

The two species are closely allied and seem to intergrade. Two additional forms have been segregated, *F. villosa* (Rydb.) Eastwood and *F. lessingii* Mey. and Walp. These approximate *F. chamissonis* in range. Several hybrids have been reported (Rydberg, 1922).

The tribe *Ambrosieae* of the *Compositae* comprises genera mostly American, and especially North American. *Franseria* occurs mainly in western North America and northern and central Mexico, with a very few species in South America (Hoffmann, 1894). Rydberg's treatment of the genus (1922), in which rather minute splitting is evident, recognizes 39 species in North America. The generic center comprises Arizona, southern California, and Baja California. The last named possesses the greatest number of species.

Tanacetum douglasii DC. and *T. camphoratum* Less. (fig. 6*j*) are frequent members, within their ranges, of the foredune community. The first is most abundant on the coast of Washington and Oregon; a few records indicate its presence on Vancouver Island and the Queen Charlotte Islands. The second occurs on the coast of Oregon and California, frequently as far south as Humboldt Bay, with an outlying station at San Francisco. The Pacific Coast species have been frequently confused with the eastern *T. huronense;* because there has been no opportunity to make a critical study of the doubtful specimens, the ranges of the two Pacific species have been combined in figure 6*j*.

Following Rydberg's treatment of the genus (1916), we find

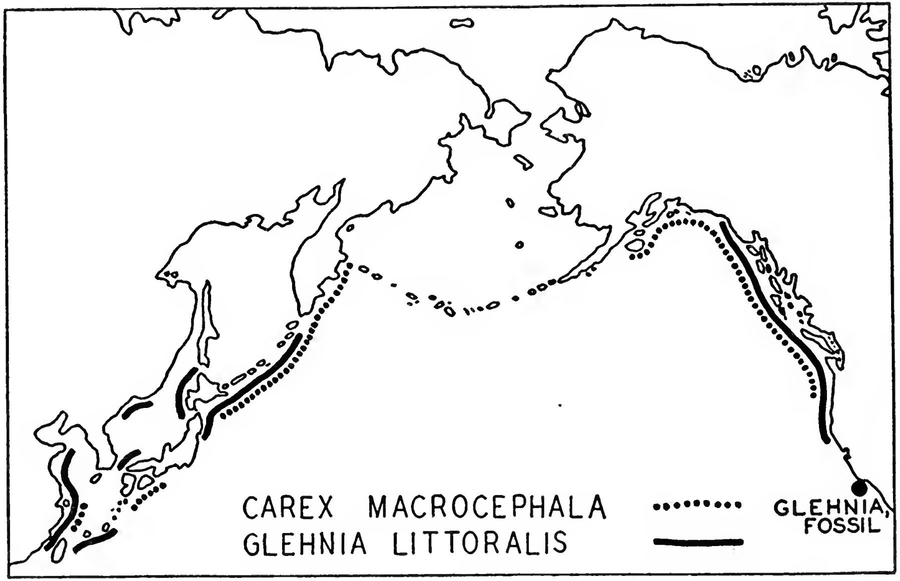

Fig. 7. Species occurring on both the American and the Asiatic coasts of the Pacific Ocean.

four species of *Tanacetum* native to North America—the two Pacific species, *T. huronense* Nutt., ranging from New Brunswick and Maine to the Great Lakes and Hudson Bay, and *T. bipinnatum* (L.) Schultz, occurring from the lower Mackenzie River westward through central Alaska into eastern Siberia, and, according to Fernald (1923), across northern Asia to Russian Lapland. All four species are closely similar. Fernald suggests that *T. huronense* may fairly be considered a variety of *T. bipinnatum*. All but *T. bipinnatum* are rather strictly coastal, except that *T. huronense* is also found on the shores of the Great Lakes.

SPECIES OF STABLE DUNES

Dominants.—Eriogonum parvifolium Sm. (fig. 8*a*) is an important dominant in the dune shrub community throughout its range, which extends from San Francisco to the Mexican boundary. It sometimes strays inland a short distance, and occasionally occurs in habitats other than dune sand, such as bluffs and terraces. The large genus *Eriogonum* is confined to western North America, where its members are conspicuous features of the vegetation in semiarid regions. The present species belongs to a group composed mainly of shrubs. A close relative is *E. fasciculatum* Benth., one of the most important dominants of the coastal sagebrush climax of southern California.

Lupinus arboreus Sims (fig. 8*b*) is not confined to dune sand. It occurs in all sorts of sandy places, and is occasionally found at considerable distances inland. It is hardly a typical member of the dune shrub community. It ranges from Humboldt Bay southward to Ensenada, Baja California.

Lupinus chamissonis Eschsch. (fig. 8*c*) is one of the most characteristic dominants in the dune shrub community. It is common from Marin County to southern California. There is

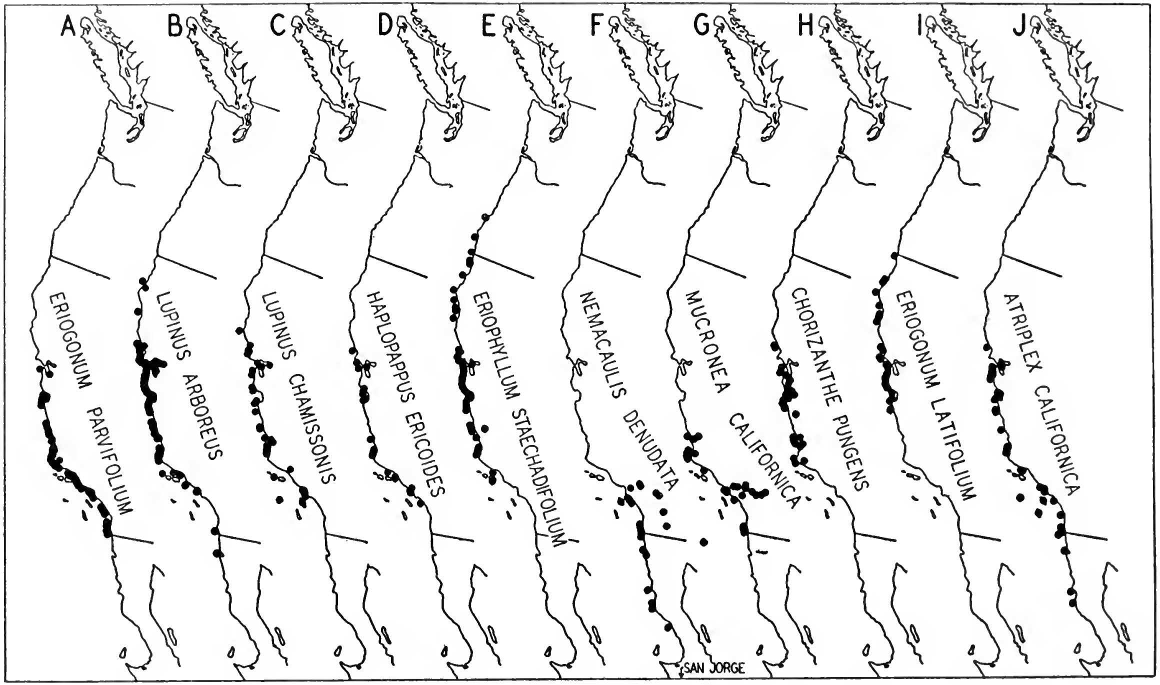

Fig. 8. Species of stable dunes: dominants (*a-e*); subordinates (*f-j*).

also a record from Point Arena. The southernmost recorded occurrence on the mainland is at Redondo, Los Angeles County. It is found also on the islands off the coast of southern California. Numerous specimens from interior stations in southern California and in Oregon are probably not of this species. There has been no opportunity for critical study of these, and they are not recorded on the map. It seems clear that *L. chamissonis* is a coastal representative of a small complex of forms, mostly shrubs, ranging over the southern Coast Ranges and southern California. The other species recognized by Smith (in Jepson, 1925) are *L. longifolius* (Wats.) Abrams and *L. albifrons* Benth., the latter including several varieties.

Haplopappus ericoides (Less.) H. and A. [*Ericameria ericoides* (Less.) Jepson], figure 8*d,* is one of the two most characteristic dominants of the dune shrub community of the central California coast; it is a constant companion, within its range, of *Lupinus chamissonis.* It extends from Bodega Point, Sonoma County, to Los Angeles. Very rarely does it stray inland, but sometimes it grows on soils other than dune sand. For this species we have available, in the work of Hall (1928), a thoroughly adequate discussion of taxonomic and genetic relationships. This provides the best possible illustration of speciation in the coastal belt from adjoining inland stock, and therefore a detailed presentation is justified.

The genus *Haplopappus,* as conceived by Hall, is a very large, complex group which has usually been divided into a number of separate genera. Hall summarizes its history as follows. All available evidence suggests Mexico as the point of origin. In time came a separation into two groups, one now confined to North America, the other to South America. Among the North American species the section *Ericameria,* to which *H. ericoides* belongs, occupies high phylogenetic rank. The subgroup containing *H. ericoides* comprises four closely related species. *H. pinifolius* Gray and *H. palmeri* Gray are important members of the coastal sagebrush of southern California. *H. eastwoodae* Hall presents an interesting problem. It is a closely restricted endemic in the vicinity of Monterey and Carmel, and is so like the widely ranging *H. ericoides* in superficial appearance and habitat that it was not recognized until 1904. Mutant origin is at once suggested, but, according to Hall, its fundamental characters are more primitive than those of the other three members of the group. "It is possible that it is either a representative of the primitive *Ericameria* or a reversional derivative of *H. ericoides*" (*op. cit.*, p. 260). The latter alternative seems the more plausible.

Haplopappus ericoides is placed at the apex of its line. The situation is best presented in Hall's words (*op. cit.*, p. 264):

> All of the evidence points to the conclusion that *Haplopappus ericoides* occupies a high phylogenetic position. Although of close consanguinity with *H. pinifolius* and *H. palmeri*, it possesses certain unique features which almost certainly stamp it as a type more advanced than either of these. . . . In geographic position, as in phylogenetic, this species has reached the frontiers, for it is restricted to dunes and sandy soil along a narrow belt near the coast of southern and middle California. This limitation of a highly modern type to a narrow geographic area . . . is in line with the requirements of the age and area hypothesis of Willis; but it may be questioned if the restriction of the present species may not be due to inability to compete with others outside its own peculiar edaphic and climatic habitat. This inability may in turn be accounted for by the absence of variation within the species, which is thus seen to suffer from its own high specialization.

Eriophyllum staechadifolium Lag. (fig. 8*e*) is of lesser importance than the other dominants of the dune shrub community. It is more apt, also, to be found in sand that is not entirely stabilized. It ranges from Bandon, Oregon, southward to Santa Barbara and Santa Cruz Island, California. The genus *Eriophyllum* ranges from British Columbia to Baja California and eastward to Montana, Wyoming, Nevada, and Sonora. Two-thirds of the species are confined to the California Coast Ranges and the lower altitudes of the Sierras (Rydberg, 1915).

Subordinates.—Nemacaulis denudata Nutt. (fig. 8*f*) is an unimportant annual herb which grows in semistabilized sand along the coast from San Pedro, Los Angeles County, south into Baja California. The record farthest south is from San Jorge, N Lat. 26°. It is also found inland in southwestern Los Angeles County, along the western edge of the Colorado Desert, and in southwestern Arizona. The genus is monotypic.

Mucronea californica Benth. (fig. 8*g*) and *Chorizanthe pungens* Benth. (fig. 8*h*) are small annuals which cover extensive areas of stable sand where the shrubs grow sparsely. *Chorizanthe* has the more northerly range and is more closely confined to the coast. It is found from Bodega Point, Sonoma County, southward to Point Conception. The range of *Mucronea* slightly overlaps that of *Chorizanthe;* it extends from Morro, San Luis Obispo County, southward to the Mexican boundary and inland to the upper Salinas Valley and the San Bernardino Valley. The genus *Chorizanthe* occurs in western North America and in northern Chile west of the Andes (Reiche, 1907; Goodman, 1934). In North America it is mainly typical of the deserts and arid foothills of southern California. The small genus *Mucronea* seems to center in southern California.

Eriogonum latifolium Sm. (fig. 8*i*) often precedes the shrubs on recently stabilized sand. It is strictly littoral, ranging from Point St. George, Del Norte County, southward to Point Sur, Monterey County.

Atriplex californica Moq. (fig. 8*j*) is a minor species in the dune shrub community and occurs also in brackish areas bordering salt marshes. It ranges from Bodega Point, Sonoma County, southward to Cedros Island, Baja California. It is not closely related to any other North American species of the genus, but seems to be derived from ancestral stock no longer represented (Hall and Clements, 1923).

Cardionema ramosissima (H. and A.) Nelson and MacBride [*Pentacaena ramosissima* H. and A.] (fig. 9*a*) is a prostrate perennial which grows on bare sand that is more or less stabilized. It ranges from Moclips, Washington, southward to Rosario, Baja California. The genus is principally of western South America, where it is not exclusively coastal. Our species occurs upon the coasts of Chile and Ecuador.

Erysimum capitatum (Dougl.) Greene (fig. 9*b*) is a comparatively infrequent subordinate in the dune shrub community, there producing erect, sparsely leaved stems as much as two feet high. It also grows close to the shore on partly stabilized sand, where it assumes a very different habit, becoming a typical rosette plant with closely placed leaves lying flat upon the sand and a practically sessile flower cluster. It ranges from Point St. George, northern California, southward to San Diego County. The genus *Erysimum* has had no satisfactory taxonomic treatment. Several species of western North America are similar in aspect to *E. capitatum*.

Potentilla lindleyi Greene [*Horkelia cuneata* Lindl.] (fig. 9*c*) is frequent in thoroughly stabilized sand. It ranges from Santa Cruz southward to Ballona, Los Angeles County, and possibly farther in both directions. For the most part it is closely confined to the coast, but var. *puberula* Jepson of southern California extends eastward to the San Bernardino Valley (Jepson,

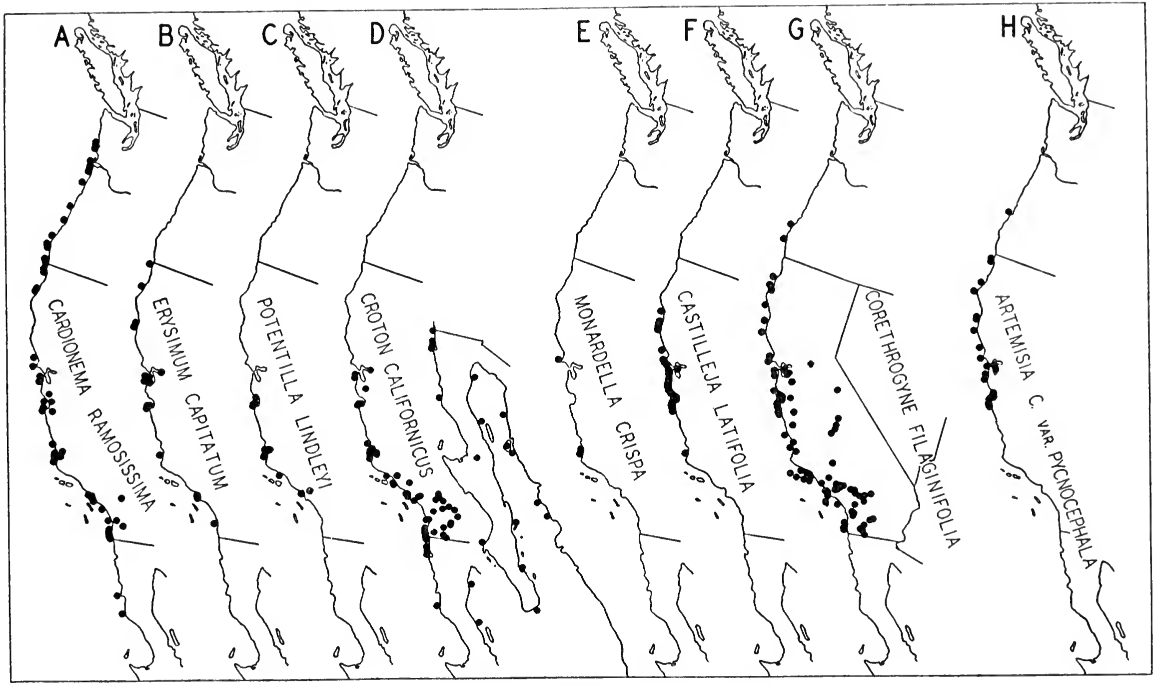

Fig. 9. Species of stable dunes: subordinates.

1925). It belongs to the subgenus (or genus) *Horkelia,* which, according to Rydberg (1898), comprises about 50 species, all natives of western North America. The group *Cuneatae* has nine species, all inhabitants of California and Baja California.

Croton californicus Muell. Arg. (fig. 9*d*) is a very abundant and typical member of the dune shrub community. It ranges along the coast from San Francisco Bay southward to the tip of Baja California. It also occurs on both shores of the Gulf of California. At the northern end of its range it is confined to the immediate vicinity of the sea, but farther south it spreads inland. It is frequent in the valleys of southern California, and is reported from scattered localities in southern Nevada, Utah, Arizona, New Mexico, and Texas. Interior stations east of California are not plotted on the map. In addition to the typical form, which is mainly coastal, Ferguson (1901) recognizes three varieties, mainly of the interior. The genus *Croton,* numbering more than 600 species, is chiefly tropical. Ferguson recognizes 24 species as occurring in the United States. These range across the southern part of the country from the Atlantic to the Pacific, several extending into Mexico. *C. punctatus* Jacq., a near relative of *C. californicus,* is a seashore plant upon the south Atlantic and Gulf coasts.

Monardella crispa Elmer (fig. 9*e*) is found with the dune shrubs and also on sand that is imperfectly stabilized. It occurs in the Santa Maria dune region, and at Point Reyes. *Monardella* is a genus of moderate size centering in California, especially in the dry foothill regions, with a few species in the central Rocky Mountains.

Castilleja latifolia H. and A. (fig 9*f*) is frequent within its range; it occurs also on bluffs, but always close to the sea. It extends from Westport, Mendocino County, south to Point Sur, Monterey County, with an outlying station at Casmalia, Santa Barbara County. *Castilleja* is an important genus in western North America, with 16 species in California (Jepson, 1925). It is represented also in eastern America, northern Asia, and South America. Another member of the genus, *C. foliolosa* H. and A., though not strictly coastal, is a frequent member of the dune shrub community.

Corethrogyne filaginifolia (H. and A.) Nutt. (fig. 9*g*) is a common and typical member of the dune shrub community. Along the coast it ranges from Bandon, Oregon, southward to the Mexican boundary. It occurs inland also, in the Coast Ranges south of San Francisco Bay, the lower and middle altitudes of the Sierras from Amador County southward, and the valleys of southern California.

The genus *Corethrogyne* is considered by Hall (1907) to be monotypic. The species is exceedingly variable. Hall recognizes eight varieties; twenty-five or more so-called species have been segregated by various authors. Certain of these occupy consistent geographic areas and others do not. The genus belongs to a group within the tribe *Astereae,* which includes such characteristic western American genera as *Aster* and *Erigeron.*

Artemisia campestris L. subsp. *pycnocephala* (Less.) Hall (fig. 9*h*) is a frequent member of the dune shrub community occurring also on sand not sufficiently stabilized for invasion by the shrubs. It is strictly coastal, ranging from Coos Bay, Oregon, southward to Point Sur, Monterey County, California. The large genus *Artemisia* is widely distributed over the northern hemisphere, and the species that have been described from North America are very numerous. In the recent treatment by Hall and Clements (1923), many of these are reduced to units of lesser rank. *A. campestris* is made up of a complex of forms, quite diverse in superficial aspect, which have been described by various authors as separate species. The species as a whole ranges over North America, Asia, Europe, and Northern Africa. Hall recognizes six subspecies, all of which have consistent ranges. Subsp. *pycnocephala* is the most distinct and is isolated in range from the others.

DISCUSSION

SPECIES OF STRAND AND SHIFTING DUNES

GEOGRAPHIC RELATIONS

Of the 25 species of strand and moving dunes, 12 range beyond the region under discussion in various directions, and 13 are endemic. The 12 with extraterritorial ranges fall into five groups. Discussion of these and of the endemics will be followed by generalizations concerning the origins of the strand and shifting dune flora.

1. *Species with more or less perfect circumpolar distribution, ranging various distances southward along the coasts of the Atlantic and Pacific.*

Elymus arenarius
Honckenya peploides
Lathyrus japonicus
Mertensia maritima

We have no certain knowledge of the preglacial distribution of the species of this group. We may, however, point to certain places where they may have survived during the period of Pleistocene glaciation. The southern parts of their coastwise ranges on the Atlantic and Pacific immediately suggest themselves. In addition, there is no apparent reason why they may not have lived upon the Arctic coasts of America and Siberia. In Alaska, except in the southern part, the lowlands and shores were ice-free. *Elymus, Honckenya,* and *Mertensia* live today upon the shores of Greenland, where the edge of the ice sheet lies very close to the sea. Much of the arctic archipelago was unglaciated, but here conditions must have been almost prohibitive in their severity. In Siberia, Kamchatka and the Taimyr Peninsula were glaciated (Woldstedt, 1929), but the arctic coast as a whole was probably free of glacial ice. The extended and fairly continuous ranges of today strongly suggest a wide preglacial distribution and re-advance from several centers. As the ice sheets receded, these species probably moved forward almost as fast as the shores became open to colonization. In Glacier Bay, Alaska, at the present time, *Elymus* and *Mertensia* are following less than half a century behind the disappearance of the ice. *Honckenya* and *Lathyrus* invade somewhat more slowly (Cooper, 1931). On the Pacific coast of North America there was advance southward from arctic Alaska and northward from Washington. For *Mertensia* it seems almost necessary to assume an arctic center, for its present range ends at the Queen Charlotte Islands. On the Atlantic coast of North America, invasion was probably from the south, and it was doubtless from here that *Elymus* and *Lathyrus* reached the region of the Great Lakes. The arctic coast of Canada may well have been invaded both from the Atlantic and from Alaska. In Europe the southern Atlantic coast must have been the starting point, although for *Elymus* and *Honckenya* arctic Siberia also may have been a center. For all species except *Honckenya,* the present ranges on both sides of the Atlantic lie entirely within the glaciated regions, so that these ranges must have shifted bodily northward. This is a perfectly reasonable assumption; the range of *Glehnia* actually underwent such a movement. Distribution of the species of the group on the Pacific coast of Asia may not have been seriously disturbed during the Pleistocene. *Elymus* and *Honckenya* have most nearly regained their assumed preglacial territory. There is an apparent break in *Mertensia* across arctic Siberia, which may never have been occupied; in *Lathyrus* there is a gap across arctic Canada as well.

It is of interest to note that upon the coast of southern Alaska and British Columbia, where glaciation must have completely exterminated plant life, all four species have effected a fairly thorough reoccupation. They grow wherever suitable habitats occur. This has been possible because they are primarily inhabitants of the upper beach and not dependent upon accumulations of dune sand.

All four species have given rise to varietal forms in different parts of their extensive ranges, the most important of which have been noted in a previous section. Doubtless some of these have arisen in connection with the Pleistocene interruption of their ranges; satisfactory treatment of this problem must await more detailed knowledge.

2. *Species with close relatives on the Atlantic coast of North America and in central Alaska and eastern Siberia.*

The two species of *Tanacetum* comprise this small group. They resemble the species of the first group, especially *Elymus* and *Lathyrus,* in being represented by very closely allied forms on the Atlantic coast of North America, the Great Lakes, and in Alaska and eastern Siberia. The group, however, does not extend to Europe and is not present on the arctic and subarctic coasts of America. Moreover, the species of Alaska and Siberia is not coastal. The point of origin cannot be determined, but it seems clear that a formerly continuous range was broken up by glaciation. The present-day forms may well have arisen through isolation.

3. *Species occurring also on the coasts of eastern Asia.*

This group comprises two species with remarkably similar distribution: *Carex macrocephala* and *Glehnia littoralis.* Their ranges on the American and Asiatic coasts correspond rather closely; both are absent from the Alaska Peninsula and the Aleutian Islands. On the American coast both are abundant south of the glacial boundary and occur on Vancouver Island. North of there, they have been found in only a few scattered localities, partly because exploration has been incomplete, but principally because suitable habitats along this coast are few and widely separated. Both species require accumulating sand. Northward invasion of the glaciated region has thus been difficult and slow. The fossil record of *Glehnia* 400 miles south of its most southerly station of today, in connection with its invasion of the glaciated area, proves that the range of this species has shifted bodily northward in postglacial time. It is reasonable to assume that the same thing has happened to other plants, for example: *Carex, Tanacetum, Elymus, Honckenya, Lathyrus.* The ultimate origin of *Carex macrocephala,* with no near relative in its very cosmopolitan genus, is veiled in mystery; *Glehnia* seems quite certainly to be descended from American stock. Another parallel between the two is that both have developed, under isolation, into pairs of forms, Asiatic and American, that may be specifically distinct.

4. *Species occurring also in South America.*

Juncus lescurii
Carpobrotus chilensis
(also Lathyrus japonicus)
Fragaria chiloensis

Though similar in present range, these species have had quite diverse histories. *Juncus* is an almost cosmopolitan genus, but *J. balticus,* probably the closest relative of *J. lescurii,* is mainly of the northern hemisphere. *Fragaria chiloensis* also belongs to a genus that is typically northern. The same is true of *Lathyrus japonicus,* which, although found in South America, falls more naturally into group 1. *Carpobrotus chilensis,* on the contrary, belongs to a group centering in South Africa which has spread eastward and westward, finally reaching our territory by way of South America. It is the only species that has certainly entered from that direction.

5. *Species of general distribution upon subtropical coasts.*

Convolvulus soldanella, the most widely distributed of all our strand species, is, judging from the general range of the family, of subtropical origin.

6. *Endemics.*

The species of this group, confined to the area under discussion, show various extraregional affinities. The following eight species are quite definitely derived from stock which has long inhabited the more or less arid parts of western America:

Atriplex leucophylla
Abronia latifolia
Abronia maritima
Abronia umbellata
Lupinus littoralis
Oenothera cheiranthifolia
Franseria bipinnatifida
Franseria chamissonis

The remaining five represent genera mainly north temperate in distribution, present in western America but not characteristic of the adjoining arid regions:

Poa confinis
Poa douglasii
Poa macrantha
Polygonum paronychia
Lathyrus littoralis

From the analysis here presented, the following generalizations concerning the origins of the flora may be made.

Fourteen species of eleven genera, some endemic, some with extraterritorial extensions of range, are of subarctic or north temperate origin:

Poa confinis
Poa douglasii
Poa macrantha
Carex macrocephala
Elymus arenarius
Juncus lescurii
Polygonum paronychia
Honckenya peploides
Fragaria chiloensis
Lathyrus japonicus
Lathyrus littoralis
Mertensia maritima
Tanacetum camphoratum
Tanacetum douglasii

Nine species of six genera, all (except *Glehnia*) endemics, are derived from the neighboring arid and semiarid hinterland:

Atriplex leucophylla
Abronia latifolia
Abronia maritima
Abronia umbellata
Lupinus littoralis
Oenothera cheiranthifolia
Glehnia littoralis
Franseria bipinnatifida
Franseria chamissonis

The remaining two species have entered from South America or the subtropics:

Carpobrotus chilensis
Convolvulus soldanella

FEATURES OF LOCAL DISTRIBUTION

Species density.—Maximum species density occurs from middle Oregon to Mendocino County, California. Within this stretch 22 of the 25 species occur, with a maximum number of 19 at any one point. The only species not present within this strip are *Carex macrocephala, Abronia maritima,* and *Mertensia maritima.* Northward we find a species density of 18 as far as Cape Flattery, beyond which there is a sharp decline to 8 at the center of Vancouver Island. Farther north there is a very gradual decrease to a minimum of 5 in southern Alaska. South from Mendocino County, decrease is fairly regular. The only exception is in the vicinity of Monterey Bay, where there is a sudden drop from 14 to 10. At the Mexican boundary the species density is 7; at Socorro, 5; and beyond Bahía de Sebastián Vizcaino but 1 species, *Abronia maritima,* remains. As far as Socorro, no compensating strand plants appear to replace those dropping out, except that *Allenrolfea occidentalis* (Wats.) Ktze. and species of *Salicornia* tend to become builders of foredune hillocks. Certain tropical strand species appear farther south—for example, *Ipomoea pes-caprae*—but the extent and character of the strand flora of the Mexican coasts is not at present ascertainable.

In more general view, the region of high species density may be considered as extending from southern Vancouver Island to Monterey Bay. Yet this is by no means the region where the greatest number of individuals of the type appear. Foredune hillocks, accurate indicators of the number and vigor of these species, are almost absent on the Oregon coast. They become gradually more evident southward, and attain their greatest development in southern California, where species are comparatively few but individuals are abundant.

Two factors may provide an explanation. Constant and severe summer winds in the north are inimical to foredune formation both because they make accumulation of sand difficult and because they increase transpiration from the plants. Again, in the north, frost kills back the plants in winter, so that accumulations made during the summer are dissipated, whereas in the south growth is continuous and the hillocks constantly tend to increase in size. Particularly important in the south are the frost-sensitive succulents *Abronia, Carpobrotus, Convolvulus,* and *Franseria,* which there are able to flourish throughout the year.

Effects of barriers.—For the most part, upon the coast of the United States and Baja California the strand-dune environment occurs in strips of varying length separated by bluffs, cliffs, bays, and rivers. Most of the interruptions are short and obviously ineffective as barriers to coastwise migration. It is conceivable that a break in the environment of considerable magnitude might be effective. The Santa Lucia mountain range constitutes such a possibility, because it presents a precipitous face to the sea fifty miles in length, with very few and insignificant accumulations of sand. At the northern end five species reach their southern limits —*Poa douglasii, Elymus arenarius, Polygonum paronychia, Lathyrus littoralis,* and *Franseria chamissonis.* A similar but less imposing stretch of cliffs in southern Humboldt and northern Mendocino counties has no effect at all.

North of the Canadian boundary the situation is very different. Here, owing to the abruptly mountainous coast and oversteepening of slopes caused by glaciation, suitable habitats for strand plants are the exception rather than the rule; they are of limited extent and separated by wide distances. The abrupt drop in species density near the glacial boundary is surely significant. Species from the south have invaded or reinvaded the glaciated area for a slight distance only or not at all. No more than two species dependent on accumulating sand—*Carex* and *Glehnia*—have gone far north, and these, so far as collections show, have established themselves at only a few points. *Elymus, Honckenya, Fragaria, Lathyrus,* and *Mertensia,* requiring merely beach conditions, are much more thickly distributed. Fewness and wide separation of favorable habitats, together with shortness of available time, has certainly been effective in hindering northward migration. Climate can have borne no causal part in this, for there is no sudden change in any factor corresponding with the abrupt drop in species density.

Climate, however, must be effective in a more general way in limiting the ranges of species, here as elsewhere. Freezing temperatures doubtless set potential limits to northward migration of sensitive southern species, but south of the glacial boundary, as I have pointed out, the effect of this factor is merely to convert potential ever-growers into winter-dormant perennials. Increasing dryness southward may be a factor in the elimination of certain species. Those ranging farthest south are superficially the most xeric.

COMPARISON WITH THE ATLANTIC COAST OF NORTH AMERICA

Two facts stand out clearly: likeness between the floras of the two coasts in the north, and unlikeness in the south. All four species in the subarctic group are present also on the northern Atlantic coast, together with a closely allied species of *Tanacetum*. Three of these five range farther southward on the Atlantic coast: *Mertensia*, 10°; *Honckenya*, 7°; *Lathyrus*, 1°. *Elymus* goes 5° farther south on the Pacific coast. The ranges of *Tanacetum* on the two coasts are closely similar. There are but two important strand plants on the northern Atlantic coast that are not native on the northern Pacific, and both of these have become naturalized there. *Cakile edentula* already behaves like a native, and *Ammophila arenaria* is fast making itself thoroughly at home. Four species of the northern Pacific coast are not native upon the Atlantic: *Carex macrocephala, Juncus lescurii, Fragaria chiloensis,* and *Glehnia littoralis.* It is of interest that the Asiatic form of *Carex macrocephala* has become established in one or two places on the New Jersey coast and is spreading rapidly (Fernald, 1930).

The general strand flora of the southern Atlantic coast differs absolutely from that of the southern Pacific. Five genera—*Carex, Polygonum, Atriplex, Croton, Oenothera*—occur in common, but the parallel is no more than a coincidence.

SPECIES OF STABLE DUNES

Of the eighteen species in this group, representing sixteen genera, all but two are endemic. *Cardionema ramosissima* occurs also in western South America; *Artemisia campestris* var. *pycnocephala* is excluded from the list of endemics solely because of the wide concept of the species here adopted. The group is not so strictly coastal as are the strand species. *Nemacaulis denudata, Mucronea californica,* and *Cardionema ramosissima* occur also in the lowlands of southern California, *Corethrogyne filaginifolia* is found there and in the south Coast Ranges and Sierras, and *Croton californicus* in the Great Basin and eastward to Texas.

Six of the genera represented—*Eriogonum, Eriophyllum, Nemacaulis, Mucronea, Monardella, Corethrogyne*—are confined to western North America. If a narrower view of generic limits were adopted, *Horkelia* (*Potentilla*) and *Ericameria* (*Haplopappus*) would be added to this group. *Lupinus* and *Castilleja,* though not confined to western North America, attain their greatest development there. *Atriplex, Croton,* and *Artemisia* are widespread, but all are abundantly represented in western America. *Chorizanthe* and *Cardionema* occur also in South America.

It is quite evident that almost all members of the group are of local origin. Differentiation within certain important genera of the arid interior has given rise, along the coast, to forms more or less strictly confined to the ocean shore. Two genera, *Nemacaulis* and *Corethrogyne,* are monotypic; in the latter, however, there has been differentiation into a multitude of minor forms more or less distinct. Both are so closely connected with related genera that we are justified in assuming local origin. All but one species of the group must therefore be placed with the list of nine species of strand and shifting dunes to which local origin has been assigned. *Cardionema ramosissima* alone, like *Carpobrotus chilensis,* seems to have originated in South America.

SUMMARY

The flora of strand and dunes on the Pacific coast of North America comprises two groups distinguished by environmental preferences: (*a*) species of strand and shifting dunes; (*b*) species of stabilized dunes. The latter constitute a distinct community only on the southern portion of the coast; the corresponding vegetation in the north is not of a strictly maritime type.

A province such as the one here treated, linear in form, frequently interrupted, unstable in the extreme, cannot be expected to be a center of evolution, to give rise to a distinctive flora, to become a focus for centrifugal migration. Instead, the population of such a province is made up in part of species differentiated from neighboring inland stock in response to the special conditions of the shore, and in part of species that have migrated, mainly along the shore, from other maritime provinces where they have been differentiated from inland stock.

Thus, on the Pacific coast of North America we find first, a group of 26 species definitely derived from stock of the local hinterland, representing either genera confined to the region or local sections within widespread genera. This group includes one-third of the species of strand and moving dunes and practically all those of stabilized dunes. The genera represented are mainly characteristic of arid and semiarid habitats. Of the remaining 17 species, 14 (all of strand and moving dunes) are of subarctic or north temperate origin. Most of the genera which these species represent occur in the neighboring regions inland, but are widespread, and their local representatives are not closely

related to the maritime species. Three species (2 of shifting, 1 of stabilized dunes) are derived from the subtropics and South America.

Considering the strand and shifting dune flora alone, species density is greatest in southern Oregon and northern California. This center does not correspond with the region where the greatest number of individuals occurs, which is in southern California. In the unglaciated portion of the coast, physiographic barriers to migration have been of slight importance. In the glaciated region, fewness and wide separation of suitable habitats, combined with shortness of available time, have greatly hindered reinvasion. The strand floras of the Atlantic and Pacific coasts of North America are strongly similar in the north and entirely different in the south.

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* Limitation of space forbids citation of the numerous publications from which distributional data have been derived.

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The Genetic Phytogeography of the Southwestern Pacific Area, with Particular Reference to Australia

By Ludwig Diels

From the time of J. D. Hooker's famous Introductory Essay, On the Flora of Australia, its Origin, Affinities, and Distribution (1859), it has been known that a large, Autochthonian element was a prominent feature of the Australian flora, and that there were strong Indo-Malayan affinities and some relations to the antarctic regions.

This evidence appeared to favor the assumption that Australia had been isolated for a long time, that it had had early connections with the Malayan Archipelago, and that more recently it had been influenced by the south. Some years ago, however, this doctrine was challenged by Wegener in his well-known theory of the displacement of the continents.

According to his idea, there was, in Palaeozoic times, a universal continent Pangaea. In the middle Jurassic, Antarctica-Australia began to separate from this continent and to drift southeastward. It was still connected with South America in the early Tertiary. Not until the older Quaternary did Australia separate from Antarctica and move northward, and, even at that time, a deep sea existed between Australia and the Malaysian Archipelago.

Now, if Australia had been joined to the southern regions for the long time from the beginning of the Tertiary period to the first part of the Quaternary, namely, during the epoch of the evolution of Angiosperms, the southern element would be dominant in the Australian flora. Let us see whether this is the fact.

This southern element contains two layers of somewhat different character. The first is the Antarctic element *sensu strictiore.* It is composed of microthermic plants growing in southernmost South America, on the subantarctic islands, and on the higher mountains of New Zealand, Tasmania, southeastern Australia, and New Guinea. These species have been listed by Hooker, Engler, Alboff, Skottsberg, and others. Skottsberg, the last author to treat them exhaustively, finds 49 natural orders represented in the Antarctic class; it is to be kept in mind, however, that the affinities of all these plants are not yet settled. It is an important fact that nearly all the Antarctic species in Australia have been found in the southeastern part (including Tasmania) only, and that these species are represented also in New Zealand, at any rate by vicarious forms. Both countries seem to have been fed from the same regions, situated between S Lat. 50° and 60° at a period when access was easier than at present.

Another layer of the southern element contains species which need more warmth than the true Antarctic plants. They are present in lower altitudes and latitudes of Australia, New Guinea, New Caledonia, and New Zealand. Because they are taxonomically more distinct from one another than are the true Antarctic species, they are considered older types. Examples are offered by Araucaria, Podocarpaceae, Cupressaceae, Monimiaceae, Escallonioideae, and Cunoniaceae. The area of a number of these types is similar to that of the Antarctic species so far as they are restricted to eastern Australia. Many genera, however, spread to New Guinea, Melanesia, and often to the Malayan islands or even more distant regions. Others are distributed all over the Australian continent (Callitris), or are found in southwestern Australia (for example, Podocarpus, Aphanopetalum). From these facts it is obvious that these genera are no recent immigrants, but old inhabitants of the continent. They belong to the Autochthonian element of the Australian flora. Their existence proves that the Autochthonian flora included members of groups which, at the present day, are distributed principally in the southern hemisphere, but it is impossible to infer that they originated in the south.

A great many genera of the Autochthonian element of the flora of Australia (often including New Guinea, Melanesia, and New Zealand) do not display any clear affinities, namely:

Liliaceae § Johnsonieae
Liliaceae § Lomandreae
Liliaceae § Calectasieae
Liliaceae genus Hewardia
Haemodoraceae genus Haemodorum
Amaryllidaceae § Conostylideae
Amaryllidaceae genus Campynema
Orchidaceae § Diurideae
Santalaceae § Anthoboleae
Proteaceae § Persoonioideae
*Balanops
*Eupomatia
*Himantandra
Saxifragaceae genus Eremosyne
Saxifragaceae genus Tetracarpaea
Saxifragaceae genus Bauera
*Byblis
Rosaceae genus Stylobasium
Leguminosae § Podalyrieae
*Cephalotus
Tremandraceae
Euphorbiaceae § Stenolobeae
Sapindaceae § Dodonaeaceae
Stackhousiaceae
Thymelaeaceae genus Pimelea
Passiflora § Disemma
Myrtaceae § Chamaelaucieae
Halorrhagaceae genus Halorrhagis
Umbelliferae § Xanthosiinae
Epacridaceae
Scrophulariaceae genus Duboisia
Scrophulariaceae genus Anthocercis
Labiatae § Prostantheroideae
Rubiaceae genus Opercularia
Goodeniaceae
Stylidiaceae
Compositae genus Olearia
Compositae genus Calotis
Compositae genus Lagenophora
Compositae genus Brachycome
Compositae § Angiantheae

This list contains not only isolated monotypic genera (*), but also polymorphous groups. We do not know where to look for their affinities, and this corroborates the opinion that they were separated from other tribes at an early date. Hence it appears that Australia, where they were evolved, was isolated for a considerable length of time and not connected with southern regions during this important period of its history.

Thus, for the southern element of the Australian flora, I find:

(1) That in eastern Australia, several true Antarctic genera and species are found which may date from late immigrations.

(2) That only a very few other southern threads appear in the tissue of the Autochthonian flora.

(3) That in the overwhelming majority of this Autochthonian flora, no southern relations are indicated.

These data are not compatible with the principal assumption of Wegener's theory that Australia had drifted to the north quite recently, and had approached the continental block of south-eastern Asia only yesterday.

In order to test further the value of this assumption, it will be useful to examine the Asiatic or Malesian elements in the flora of Australia.

Such Asiatic features present themselves in the more distant relations of some Autochthonian genera, namely:

Casuarina
Chenopodiaceae § Kochiinae
Chenopodiaceae § Atriplicinae
Acacia § Phyllodineae
Eucalyptus
Sterculiaceae § Buettnerieae
Myoporaceae genus Eremophila
Rutaceae § Boronieae

In Casuarina and Acacia § Phyllodineae, it is doubtful whether the species indigenous in Malaysia originated in Australia, or, on the contrary, whether the Australian species originally came from the north. In other genera (Rutaceae § Boronieae, Eucalyptus), the evidence is in favor of the northern origin, the Boronieae being specialized Xanthoxyleae, and the genus Eucalyptus a progressive derivative of the Malesian Syzygium type.

The argument deduced from the genetic resemblance of such genera is strengthened by a great many examples of relations which, in analyzing the flora, we recognize as Malaysio-Australian. These relations are found not only in orders peculiar to the Palaeotropics (for example, in Pandanus and Musa), but also in many orders common to Asia and America. Even here the Australian genera or species are more closely allied to the Asiatic forms. This is true for:

Cycadaceae
Palmae
Araceae
Dioscoreaceae
Zingiberaceae
Anonaceae
Monimiaceae § Mollinedieae
Menispermaceae § Cocculinae
Simarubaceae
Loganiaceae
Gesneriaceae

The same feature is to be observed in many endemic genera of the Australian flora.

From this fact it is evident that these relations are not attributable to recent events, but to conditions of a more remote period. This is confirmed by the extension of, for example, Pittosporaceae, Pritzelia, and Dioscorea hastifolia to the central parts of the continent and to southwestern Australia.

Therefore, the connection between Malaysia and Australia must have lasted for a long time in different forms, and may continue to the present day, at any rate in species with efficient means of distribution. As a consequence, this Malaysian component comprises groups of each degree of classification. There are numerous genera distributed from southern India to eastern Australia, and even many species are found everywhere from the

Malay Peninsula at least to Queensland. Not a few of them may have increased their area by the help of man, spreading with him to the east. But this cannot apply to all; we must assume that such genera as Nepenthes and Terminalia, and such orders as Sapindaceae, Asclepiadaceae, and Rubiaceae, reached the boundaries of their extension by the natural means of propagation, even though this happened perhaps only a short time ago.

From the character of the Malaysian elements, it is apparent that there were connecting pathways from early times. We know that the situation and the condition of these pathways changed, and that they were impassable at certain times and in certain sections. For this reason, the relations between Malaysia and Australia do not appear in all groups of animals and plants in equal manner and in equal strength. But there is no doubt that the degree and the variety of those relations do not agree with the assumption of the displacement theory that Australia entered into connection with Asia only at a late date. If that hypothesis were correct, no peculiar Australian groups of Malaysian affinity would exist. The Malaysian component would prove to be modern. As a matter of fact, such peculiar groups are by no means missing. The whole Malaysian component is not modern, but one of its parts is. These facts cannot be explained by the notions of the displacement theory. In the modern time of earth's history, during the evolution of Angiosperms, we must assume that Australia had a position similar in relation to the other great continents to that which it holds today. An independent evolution of old groups must have been going on in Australia. Besides, influences of southeastern Asia would have commenced early and would be going on up to the present time, whereas the extensions of the Antarctic influences would have affected Australia only temporarily.

The Rôle of the Terrestrial Alga in Nature

By F. E. Fritsch

THE ESSENTIALLY AQUATIC NATURE of the plants classed as Algae is likely to cause one to lose sight of the fact that a very considerable number of these plants lead a terrestrial existence under conditions of life that differ very profoundly from those obtaining in the aquatic habitat. The majority of the terrestrial Algae are of relatively lowly organization, many being unicellular, colonial, or exhibiting a simple filamentous habit, and it is only in *Trentepohlia* and in some of the Blue-green Algae (Stigonemataceae) that indications of a higher differentiation are seen. No terrestrial alga attains to the complexity of structure and of reproductive methods met with in the advanced Phaeophyceae and Rhodophyceae. The terrestrial algal flora is essentially recruited from the classes Chlorophyceae, Xanthophyceae (Heterokontae), Bacillariophyceae (Diatoms), and Myxophyceae (Cyanophyceae), although some species of *Porphyridium* (Bangiales) are terrestrial and Pascher[34][*] has described a terrestrial member of the Chrysophyceae (*Geochrysis*).

Broadly speaking, three groups of terrestrial Algae can be distinguished: (1) those which are found between the particles beneath the surface of the soil (subterranean community),[20] (2) those which live on or just beneath the soil surface (surface community), and (3) those which live on other terrestrial substrata—rocks, tree trunks, etc.—in part well raised above the soil level (aerial community). No sharp line can be drawn between these three communities, but on the whole they are ex-

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[*] Superior figures refer to items in the bibliography at the end of this essay.

posed to increasing liability of desiccation. Nor is it possible to demarcate them rigidly from mud-inhabiting forms such as *Botrydium, Protosiphon,* etc., whose normal vegetative phase is, however, developed only in the presence of considerable quantities of moisture.* A rather special community is that which occurs amid mosses in diverse habitats and consists, in large part, of Desmids[28] and Diatoms,[2, 3] the latter differing rather markedly according to the degree of dryness of the habitat.

THE SUBTERRANEAN COMMUNITY

The subterranean community, which is found in the water constituting the films around the soil particles and occupying the smaller interspaces between them, comprises manifold species, many of which have been recorded as occurring at considerable depths.[6, 14, 15, 33, 43] In the present state of our knowledge, this community appears to be composed of a number of distinct elements.

First, it includes certain common members of the surface community. A recent investigation of naturally occuring British soils from 2- and 8-inch depths, conducted in my laboratory by Miss J. James, has shown the universal presence of *Chlorococcum humicolum* and species of *Hormidium,*† both of which are typ-

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* Yet, West's "association of irrorated rocks" (West,[49] p. 422) can hardly be regarded as terrestrial because the forms involved, although some are terrestrial, are probably normally well supplied with liquid water.

† Here should also be included moss protonema,[5] which appears almost invariably in soil cultures. Bristol[5] records *Ulothrix subtilis* var. *variabilis* as a common subterranean alga, although it has not been recorded by other investigators and no species of *Ulothrix* appeared in Miss James's cultures. I am not clear as to the nature of this species of *Ulothrix,* but strongly suspect that further study will show it to be one of the terrestrial *Hormidiums.* Similarly, I am inclined to think that the older records of the occurrence of species of *Pleurococcus* in the subterranean flora are a result of confusion with such forms as *Pleurastrum* and possibly with some of the unicellular Xanthophyceae (*Pleurochloris,* etc.), which recent research has brought to our notice. I am even doubtful whether *Pleurococcus* occurs as a member of the surface community.

ical surface forms. The species of *Chlorella, Coccomyxa, Dactylococcus,* and *Stichococcus* found in the subterranean community, although not so universally present, probably belong to the same element. Blue-green Algae (especially the species of *Phormidium*) and the majority of the Diatoms should probably also be included here.[15]

Second, there are found in the subterranean community a small number of forms which, so far as present evidence goes, are more or less characteristic of this habitat; among these are *Gongrosira terricola,* and certain Yellow-green forms (*Botrydiopsis, Pleurochloris, Monodus, Monocilia, Bumilleria,* etc.), as well as, perhaps, a few of the Diatoms. Divers of these forms have not so far been found except in soil cultures or commonly, at least, have been met with only in such cultures, suggesting the subterranean regions of the soil as the usual habitat.

The third element is what I should like to describe as the *casual* one (Bristol,[6] p. 570), including species of *Chlamydomonas, Ankistrodesmus, Vaucheria,* etc., which are only of occasional occurrence and probably owe their presence in the soil to wind-borne resting stages which fall on the surface and afterward are washed down by rain (see below, p. 201; also Fritsch[22]).

A problem of considerable interest concerns the distribution of Algae in a soil. The first serious attempt to determine this quantitatively was made by Bristol,[6] who employed a method of progressive dilution of a soil suspension, the number of organisms in each gram of soil being then computed statistically.[7] She arrived at the conclusion that there were no appreciable differences in the horizontal distribution of soil Algae in a uniform soil, but that there were marked quantitative differences in the vertical distribution. She found an abundant algal population in the top inch* and an equal or even greater number in the fourth inch, whereas samples from the two-inch and three-inch depths and from depths below four inches contained far smaller numbers. Such qualitative differences as were observed were quite irregular and appeared to be of no general significance. Moreover, by manurial treatment the proportion of the diverse Algae present can be materially altered.[27] Bristol,[6] p. 572, points out that the four-inch depth is known to be that of the greatest biological activity of most soil organisms, but it may be doubted whether such a conclusion, which refers to Bacteria, Protozoa, etc., can be legitimately extended to the pigmented Algae.

Except in the immediate neighborhood of the soil surface, the Algae inhabiting the soil must be in complete darkness, at certain times and, although in cultivated soils agricultural operations will tend to bring the deeper-living forms nearer to the surface, there is little that is apt to cause such a transference in natural soils. The activities of earthworms and other animals are perhaps more likely to lead to the destruction of the Algae than to their transference (cf., however, Esmarch,[15] p. 253). It is a well-known fact that many of the simpler Algae are capable of living in prolonged darkness and even of remaining green under these circumstances, provided that suitable organic nourishment is available. One of the most valuable studies in this respect is that of Bristol[9] on a species of *Scenedesmus* (*S. costulatus* Chod. var. *chlorelloides* Bristol-Roach) isolated from the soil. She showed that, under conditions permitting normal photosynthesis, this alga carries out no heterotrophic nutrition, whereas in diminished light intensity an increasing amount of carbohydrates is utilized and in darkness this of course is the only source of carbohydrate nourishment. However, the capacity for growth is less;

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* It is not quite clear whether this included the actual surface layer.

it diminishes progressively with increasing heterotrophic nutrition and in darkness is only about one-half that observed when full photosynthesis is maintained. As Bristol points out, there are likely to be considerable differences between different Algae in this respect[8] and, indeed, it is known that some Green Algae prosper better when organic nutriment is available than when it is not.

It is therefore credible that subterranean Algae will find a means of sustenance and even of active growth when buried in the darkness of the soil, but there are two considerations that must be borne in mind in this connection (cf. also Petersen,[38] p. 16). First, the Algae will be competing for organic nourishment with the other living organisms of the soil and it seems unlikely that this competition usually will be a successful one. Second, there is no evidence so far that the kinds of organic substances that have proved efficacious in the artificial cultivation of soil Algae are available in the soil, and there is therefore no direct proof that an alga buried in the soil in darkness will find the means of sustenance. This problem has recently been approached by Petersen,[39] who has endeavored to ascertain whether two soil-Algae (*Pleurochloris magna* and *Nitzschia Kützingiana* f. *terrestris*), inoculated into sterilized soil, exhibited any capacity for growth in the dark. His tentative conclusions are in the negative and, although the process of sterilization may conceivably have induced alterations in the nature of the organic material available, the experiment certainly affords some evidence that these two soil forms do not find suitable material for sustenance in the soil in the absence of light. Esmarch,[15] p. 259, also failed to obtain any evidence of growth in Blue-green Algae buried in the soil. These investigations show that, until definite proof has been obtained for a number of the regularly occurring soil Algae, it is not wise to conclude from experiments under laboratory conditions that such forms will be able to grow and multiply when buried in the soil, although it may well be that at certain times conditions for active growth may obtain.

For diverse reasons I am inclined to believe that the subterranean Algae are in large part, if not entirely, surface-growing forms that are washed down into the soil by heavy downpours of rain. Thus buried, they may perhaps occasionally find the necessary means of sustenance and so multiply for a time, but I think it is at least doubtful whether there is any marked activity on the part of such subterranean forms. It is significant in this connection that the most frequent of the subterranean Algae are known to be common surface forms (see also the occurrence of moss protonema), and are unicellular types with rounded cells (*Chlorococcum*) or filamentous forms that readily fragment into short lengths (*Hormidium, Stichococcus*). It is also significant that common filamentous surface forms that do not show such ready fragmentation (*Prasiola, Zygogonium ericetorum*), so far at least, have not been recorded beneath the soil surface. It is curious, however, that the soil-inhabiting Mesotaeniaceae (species of *Mesotaenium* and *Cylindrocystis*) hitherto have not been found in subterranean habitats. Esmarch[15] also arrived at the conclusion that the subterranean Blue-green flora is composed of the same forms as occur at the surface. Here the capacity to propagate by motile hormogones and the known liking for saprophytic nutrition on the part of these forms will no doubt tend to lead them to a direct penetration from the surface into the upper layers, as apparently occurs especially in cultivated and in calcareous soils.

As to the Algae mentioned above, that so far have rarely or never been found except in cultures of soil samples (*Gongrosira* *terricola, Monocilia*, etc.), it is possible that some of these are specially equipped, in a way at present not recognized, for life beneath the surface. However, it is equally probable that they, too, are actual surface forms, rarer than the others, and not so far discovered in their normal habitat. An intensive study of the surface of the soil has as yet been undertaken only in Denmark and Iceland by Petersen,[35, 37] whose investigations showed that a far larger number of surface-growing Algae exist than had previously been recognized. The same investigator[38] records two species of *Bumilleria*, hitherto mainly observed in cultures of subterranean soil-Algae (especially *B. exilis*), from the surface of soils of Hammer Bakker, and *Botrydiopsis minor* from the surface of Iceland soils.[36] These, as well as certain of the Chlorophyceae recorded, were not macroscopically visible.

It is noticeable that a considerable number of the forms so far mainly recorded from beneath the surface of the soil are Xanthophyceae (Heterokontae). Certain members of this group are known to be intolerant of strong illumination, and it is possible that the soil forms do not inhabit the actual surface, but live in the feebler light just beneath (cf. also below). This would account for their not having been observed, so far, in the study of actual surface growth.

The resting stages of aquatic Algae are known to be to a large degree wind-dispersed. Only a small proportion of such windborne spores will be deposited in other adjacent waters. Large numbers of them will fall on the soil surface and become immersed in the soil during showers of rain (Fritsch,[22] p. 254). Soil animals may also be instrumental in their burial. No doubt many such resting stages will perish without further development, but some may survive and, in my opinion, will amply account for the occurrence of the casual element among the soil Algae (species of *Ankistrodesmus, Chlamydomonas, Tribonema,* etc.). In fact, the occurrence of such aquatic types in soil cultures seems to me to provide further evidence in support of the view that the subterranean Algae are forms washed down from the surface.

I will frankly agree that it is difficult, in this interpretation of the subterranean Algae, to find an explanation for the fact, established by Bristol and referred to above, that there is often a marked increase in the population of soil Algae at the four-inch depth. This depth may, however, mark a physical boundary of some kind (for example, increase in compactness of the soil) beneath which the downward passage of algal cells occurs more slowly so that an accumulation takes place at this level. In this connection it is significant that some (though not all) of the highest numbers recorded for the four-inch depth by Bristol,[6] pp. 572, 573, followed a period of heavy rainfall.

The alternative to the view that the placing of Algae in the soil is a result of downward-washing during rain is to suppose that motile reproductive stages actively move downward in the soil and find in certain layers (namely, the four-inch level) conditions specially favorable for development and multiplication. Once buried beneath the surface in darkness, there is no apparent reason why they should not move downward as well as upward. For such forms as the species of *Chlorella* and *Stichococcus,* however, in which no motile reproductive stages occur, the only conceivable method of transference in the soil is a downward one caused by the washing effect of rain. Moreover, it still remains to be shown that, in forms such as *Chlorococcum,* zoöspores are formed within the soil; it is possible that, if reproduction occurs there, it is by means of aplanospores.

A scrutiny of the mere superficies of the soil, even in wet weather, is hardly likely to disclose all the surface-living algal growth. It is very probable that some of these forms live beneath the actual surface in a region where photosynthesis is still possible, but where better conditions in regard to moisture supply and protection from desiccation exist; also, some of these forms may be shade-loving species (see the endolithic forms referred to below). Moreover, the more specifically saprophytic forms may be influenced in their distribution by the availability of organic matter. A study of the surface community, therefore, should include not only the forms visible at the surface, but also all those encountered at depths to which light is found to penetrate. It is not improbable that a microstratification of the surface-living soil Algae may be found to obtain, depending on their immediate light requirements and on their relative degree of susceptibility to desiccation.

No data are at present available concerning the depth to which light can penetrate beneath the surface of a compact soil, but it is doubtful whether there is anything but darkness below the top few centimeters. Forms such as *Chlorococcum* and *Hormidium* appear to grow on the actual surface. How far there is direct (as opposed to passive) penetration from here into the illuminated layers of the soil has not as yet been ascertained. The forms growing at the surface are of course exposed to considerable desiccation during dry periods, and many of them become conspicuous only in wet weather. Then, however, they often appear in remarkable numbers. On peaty and sandy soils *Zygogonium ericetorum* may form an intermittent covering over acres of ground, whereas *Prasiola* and *Hormidium* often occur extensively on heavier soils, the former especially where there is organic pollution. These forms are conspicuous by virtue of the wefts which they produce. Unicellular types are more difficult to recognize unless they occur in abundance, but on damp surfaces evident growths of *Chlorococcum* may be found, and forms such as *Coccomyxa* and *Stichococcus,* though more occasional, sometimes occur in conspicuous strata; a common habitat is the basal parts of tree trunks just above the soil level.[12] Striking sheets of Blue-green Algae are seen, especially in wet periods, on cultivated soils and calcareous soils, and Petersen[37] records for Iceland extensive sheets of *Phormidium autumnale* wherever the ground is rich in organic nutriment (see also West,[49] p. 421). It remains to be discovered whether, at times when such growths are not evident on the surface, they are persisting in the illuminated subjacent layers, to aid in the resuscitation of a stratum in wet weather. The numerous forms of soil Diatoms, characterized in general by their small dimensions and their capacity for motility,[5, 35] are no doubt mainly forms living in the illuminated region of the soil, though possibly only a few are present at the actual surface.

The occurrence of a rich surface algal flora, especially in wet weather, affords, therefore, ample material from which the subterranean element can be supplied, although it is evident that the agencies bringing about downward transference operate differently on the various members of the surface community (p. 205). Bristol[6] has shown that a large proportion of the Algae in the soil are in a vegetative condition, or at least in a condition susceptible to the effects of desiccation. This is perhaps what one would expect of an Alga carried down into darkness and gradually losing its food reserves because probably its capacity to withstand drought depends, partly at least, on a high osmotic pressure and also apparently on the presence of fatlike substances.[21, 23, 29, 40, 41] It is not necessary, however, to suppose that the cells that survive are in the form of spores. The vegetative cells of diverse terrestrial Algae are known to possess a great capacity to resist desiccation,[21, 23] and the surviving cells may be those that have recently been washed downward and have not yet lost the equipment which enables them to withstand drought. In fact, if they are plentifully stocked with food reserves as a result of photosynthesis at the surface, after burial they may possibly carry on a certain amount of multiplication until these reserves are exhausted, the more so because moisture conditions will be more favorable than they normally are at the surface. But it seems highly probable that, in many instances, when the food reserves are used up, the alga is doomed to gradual death unless it falls a prey to the Protozoa present. The fact established by Johannson,[31] that the production of carbon dioxide from soils is nearly always greater during the day than during the night, would seem to imply that even the surface-living Algae are insufficient in quantity to affect materially the gas relations.

Soil Algae have been supposed to play a rôle in increasing the fertility of the soil but, clearly, if they grow and multiply at all beneath the illuminated zones of the soil, they can do so only at the expense of their own reserves or of the organic material present. In the deeper layers, therefore, they cannot increase fertility unless through their action they render certain of the organic ingredients more readily accessible to the remaining population of the soil. For this view, however, there is at present no evidence. On the other hand, the carrying down of surface forms to the deeper layers will probably add materially to the organic content of the soil because these forms have built up their bodies and no doubt have often stocked them with food reserves in an autotrophic manner. The inclusion of their substance in the soil, whether direct or indirect, must enrich it in organic material.

If the previous conclusions are correct, the importance of Algae in soil economy lies mainly in their growth at the surface, where photosynthesis is possible, and therefore an intensive study of surface-growing Algae and of their conditions of existence is in the future likely to produce results more valuable to science than a study of their occurrence in the subterranean habitat. Soil Algae have also been credited with fulfilling another function, namely, in respect to nitrogen fixation. A direct fixation of nitrogen by Algae, and particularly by Green Algae, is certainly highly unlikely, and no data brought forward in this connection have stood the test of a critical examination.[10] It is a demonstrated fact, however, that nitrogen-fixing Bacteria in cultures bind an increased amount of nitrogen in the presence of Algae. It is suggested that a possible reason for the beneficial effect of the Algae is that they remove the nitrogenous products of the activity of the Bacteria or provide in their mucilage envelopes a carbohydrate supply for the Bacteria. Clearly, however, the value of Algae in relation to nitrogen fixation beneath the illuminated zone of the soil must depend, in large measure, on their being in a condition of active growth and multiplication, and of that I believe no adequate proof has so far been presented. At present, therefore, I am inclined to doubt that soil Algae are fundamentally important to the nitrogen-fixing Bacteria except in those layers of the soil which are accessible to light and where rapid growth and multiplication of the Algae can take place.

I am fully cognizant that the suggestions presented here concerning the source and nature of the subterranean algal community, although supported by a certain amount of fact, require to be proved by diverse direct investigations. I feel, however, that there is so much that is debatable in existing views concerning the subterranean algal flora that a critical consideration of the available facts was desirable. I hope that an experimental testing of the accuracy of my suggestions will not be long delayed.

THE SURFACE COMMUNITY

In the few surface Algae that have been investigated in this connection, there is a very marked degree of adaptation to the conditions of desiccation to which they are exposed.[20, 21, 23, 40, 41] It may particularly be emphasized that they possess the faculty of withstanding drought without appreciable change and without the assumption of special resting stages. There is also evidence that they readily absorb atmospheric vapor as well as liquid water, and in this way probably are able, in large measure, to tide over periods devoid of actual precipitation and to resume active growth and multiplication as soon as wet weather sets in. The special machinery that appears to be connected with the peculiar properties of these forms has been adequately described elsewhere[20, 21, 23] and need not be dealt with here. There is some evidence to show that the special properties of such Algae enable them during periods of drought to compete successfully with the higher plants (Piercy,[40] p. 515).

Apart from the rôle which such surface-growing soil forms probably fulfill after being washed down into the soil, they must often lead to the production of surface humus after death. This must be especially true when their nature is such that they are not carried down in a living condition. Attention has also been directed (West and West,[50] p. 303) to the importance of surface wefts of Algae such as *Porphyrosiphon Notarisii* and *Zygogonium ericetorum* in consolidating the surface, and in affording in damp weather a seed bed on which smaller seeds, etc., find a ready means of germination. The rôle of surface forms as primary colonizers of new ground has frequently been emphasized.[18, 19] In this connection we may note the descriptions of the first stages in the recrudescence of growth on Krakatoa[47] and the preliminary steps in the colonization of burnt heath in England.[25] In both places what appears first is in large part a covering of gelatinous palmelloid forms that in wet weather constitutes a thin but practically continuous mucilaginous covering on the otherwise bare surface. This must aid materially in the establishment and early germination of the seeds and spores of the colonizing plants. It is probable that a more extensive study of primary colonization of newly exposed soil will show that members of the surface algal community are almost always the first to appear. To what extent such forms may also be active in the disintegration of the particles at the soil surface and immediately below it, is at present unknown.

THE AERIAL COMMUNITY

Turning last to what I have at the outset called the aerial community, I think we should include here all algal growths that do not occur on the soil proper, that is, not only those which are found on vertical surfaces (rocks, tree trunks) above the soil level, but also those inhabiting more or less horizontal surfaces of a similar nature. In all these the substratum will furnish relatively little water and the growth of Algae must be in large measure dependent on moisture obtained directly from the atmosphere. Among the most important of the rock-growing Algae are the Myxophyceae,[4, 13, 17, 18, 19, 43] the terrestrial members of which are indeed seen at their best in such a habitat; species of *Trentepohlia* also thrive but are of secondary importance, and other Green Algae and Xanthophyceae are usually quite subsidiary except apparently on some kinds of sandstone.[46] On trees the most important forms are Chlorococcales, *Pleurococcus,* and species of *Trentepohlia,* the last-named especially in the Tropics or in very humid regions such as parts of the Monterey Peninsula. A rich flora of diverse green forms sometimes occurs on trees and woodwork,[42] but as a rule the growth is very monotonous.

In respect to their rôle in nature, the rock-inhabiting forms are of special interest. Blue-green Algae in damp, mountainous tracts in temperate regions give one some idea of their capabilities for growth on rock surfaces,[13, 17] but, in order to realize their full possibilities, one must observe them in the damp Tropics. The growths there have been familiar since Welwitsch's description,[48] in 1868, of the "Pedras Negras" or black rocks of Pungo Andongo in Angola, where the dark color is caused by the prolific growth of *Scytonema myochrous* (Dillw.) Ag. var. *chorographicum* West. Bews,[4] p. 553, has described similar extensive coverings of Blue-green Algae from the Drakensberg region in Natal, where the communities of diverse Myxophyceae "cover enormous areas of the cliffs, especially the cave-sandstone cliffs and are strikingly apparent from a distance as longitudinal black strips. . . . During the very dry weather the algal covering dries up and peels from the rock in small flakes, but it does not disappear to any great extent or leave the rock again bare" (cf. also [24]), in this respect differing from the growth that Welwitsch has recorded in Angola. I myself have described similar phenomena on a smaller scale in Ceylon,[19] and McLean,[32] speaking of the Pedra da Gavea, west of Rio de Janeiro, says, "The larger part of the rock-surface is covered by blue-green Algae which form great dark stripes upon it." He also records "a species of *Trentepohlia* (*T. aurea*) which is extremely abundant on the damper patches." The so-called "Tintenstriche," recorded by diverse workers on the rocks and precipices of various mountainous tracts in Europe,[11, 13, 44] are caused by similar growths of Blue-green Algae along vertical lines down which there is a more or less constant trickle of water.

Such dense and extensive mats of aerial Algae are usually supposed to play an active part in rock erosion, and there is every reason to believe that this is correct, but at present there is little positive evidence of it. The peeling off of the growth which Welwitsch, Bews, and others describe as occurring regularly in dry weather may well act on the rock surface in a way similar to that recorded by Frye[26] for certain Lichens, but exact investigation is required. It is not known whether in all such occurrences a direct corroding effect may be exerted on the underlying rock with the help of substances excreted from the Alga, as has been established for Myxophyceae inhabiting calcareous rocks (cf. below). On horizontal rock surfaces the dense wefts or sheets (*Phormidium*) of Blue-green Algae are bound sooner or later to provide a sufficient thickness of humus for the growth of Bryophyta, Ferns, and small Phanerogams, and sometimes this no doubt also occurs in connection with more or less vertical substrata. When adequate moisture is available for a considerable length of time, successive phases of development of these mats may be traced;[18, 19] a sufficiently thick growth is established in a short space of time to afford a starting point for the development of higher types of vegetation. In short, although no doubt the rigors of the habitat often prevent development beyond the algal mat, there is every reason to suppose that a similar growth preceded the establishment of Phanerogamic vegetation in the more sheltered valleys and on the lower slopes of the cliffs where such growths are now observable on the upper parts.

On calcareous rock surfaces in the Alps and the Dolomites, Bachmann[1] and Diels[11] have recorded both an epilithic and an endolithic community of Algae, composed in large part of Chroococcales with occasional filamentous Blue-green forms and species of *Trentepohlia* (cf. also[13]). The epilithic community is confined to those points at which a slow trickle of water normally descends the rock face, whereas the endolithic community appears to be of two types. The type described by Diels inhabits very narrow, outwardly not recognizable clefts in the rocks which apparently owe their origin to atmospheric agencies. These aerial Algae may be described as chasmolithophytes.[13] They differ in general from those found on the exposed surface and are no doubt shade forms. On the contrary, the community described by Bachmann and others[13] consists of Chroococcales occupying small pits in the rock surface which are believed to result from a direct solvent action of acid excreted by the Alga on the calcareous substratum (true endolithophytes). When such growths are numerous, the surface layer of the rock to a depth of 1.5 mm. becomes quite soft and porous, so that a direct erosive action of the alga on the substratum is evident. But, even in respect to the chasmolithophytes, one cannot doubt that the presence of the Algae will lead to a gradual widening of the clefts and progressive erosion of the surface.[11]

On the whole, the chemical nature of the underlying rock does not appear to have much effect on the aerial algal community, which is apparently more influenced by the nature of the surface, the amount of available moisture, and the intensity of insolation. Frémy[17] has made a study of the composition of the aerial algal growth on siliceous and calcareous rocks in Normandy, and mentions as the only striking difference the absence of *Stigonema minutum* on the calcareous as opposed to its frequent occurrence on the siliceous rocks (cf. [46]). He points out that the hardness of the rock definitely influences the abundance and nature of the algal growth. Hard, dry rocks bear no growth at all when exposed to full insolation (cf. also[13]), but when shaded they support *Pleurococcus* and *Trentepohlia aurea,* forms which are also found on rather softer dry rocks subjected to full insolation. When shaded, these softer dry rocks bear a blue-green growth (*Gloeocapsa* spp., *Tolypothrix byssoidea* f. *saxicola, Stigonema minutum*) which, with the difference noted above, is found alike on siliceous and calcareous rocks of a certain degree of hardness. Ercegovic[13] regards *Scytonema myochrous* and *Calothrix parietina* as photolithophytes because they always occur on places exposed to strong sun. Diatoms rarely form conspicuous growths on relatively dry rock surfaces. Schade,[44] however, records yellowish brown coverings caused by *Fragilaria capucina* Desm. (cf. also [46]).

Apart from obvious algal coverings, Falger[16] has shown that Algae may also be found on rock surfaces that afford no macroscopically visible evidence of growth. He suggests that these primary colonizers prepare the way for the more obvious growths. Again Myxophyceae are dominant, although some Chlorophyceae and Diatoms are also found. Sandstone is much richer than other kinds of rocks and here, as in Frémy's observations, a direct effect of the degree of porosity of the substratum, implying a varied retention of moisture, is evident. Adequate data on the moisture content of exposed rock surfaces are, however, at present scarcely available, although Schade[44] has calculated that in sandstone the water content may amount to 12 per cent of the weight of the rock.

The forms inhabiting trees are probably of less importance in the economy of nature, but physiologically are perhaps the most highly adapted terrestrial Algae. The faculty that *Pleurococcus* possesses of withstanding extreme and prolonged drought and other unfavorable conditions is almost proverbial. According to Schmid,[45] this Alga does not stand continuous immersion in water and normally satisfies all its moisture requirements by means of atmospheric vapor. Probably the same is also true to a large degree of *Trentepohlia* (Irgang,[80] p. 15).

NOTE: This essay was completed in July, 1934. Since then Miss James's paper referred to on page 196 has been published (see Beih. bot. Centralbl., 53, A, 519–553, 1935). There has also appeared a detailed study of soil Algae by J. B. Petersen (Dansk. Bot. Arkiv, 8, no. 9, 1935) in which the author arrives at conclusions which to a considerable extent agree with those propounded above with respect to the subterranean community.

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The Plant as a Metabolic Unit in the Soil-Plant System

By D. R. Hoagland*

The relation of the plant to the soil as a medium for plant growth concerns the general botanist, the ecologist, the agriculturist, the forester, and indeed all who seek an understanding of plant growth, plant distribution, or the artificial modification of the plant's nutrient environment. But it is seldom that the soil-plant system is contemplated as a whole in its physiological aspects. Too frequently the absorbing root cells of the plant are regarded, apart from their water-absorbing functions, as merely passive receptacles for the dissolved mineral constituents of the soil. Chief emphasis is frequently placed on the solubility of these constituents in various solvents, and the quest for simple laboratory methods of evaluating soil conditions is unceasing. Single factors, for example, hydrogen ion concentration, are often assigned great weight in explanations of plant distribution or adaptation to soil conditions. Many other procedures are employed, in which some special phase of physicochemical equilibrium in the soil system is broadly interpreted in physiological terms.

Such methods of investigation do frequently yield results of local practical application, or occasionally useful generalizations, yet they are essentially nonphysiological, and therefore inadequate, in that they fail to deal with the soil-plant system as one profoundly influenced by the growth and metabolism of the

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* It is desired to acknowledge the participation of T. C. Broyer and other members of the staff of the Division of Plant Nutrition, University of California, in the experimental work cited herein.

plant itself. This latter view recognizes a system of reciprocal relations of extraordinary complexity. At times it may appear that this complexity renders hopeless the attainment of any real comprehension of the phenomena involved, but the development of methods of investigating plant growth under conditions which permit control of the principal factors in the environment of the root and shoot has renewed faith in the possibility of resolving some of the problems. Many past investigations lacking any elements of controlled experimentation have led to vast increases in observational data, and in general information, but not to secure advances in the understanding of basic principles.

The indispensability of the ecological or agricultural approach to the study of soil-plant relationships is not open to question. The whole natural environment of the plant cannot be imitated in the laboratory, and important physiological problems may first be suggested in the field. Yet the knowledge gained from observations made under natural conditions seldom suffices to establish the physiological nature of the processes involved. Such knowledge is indeed often self-limited, since new methods of studying plants in the field, and new points of view in the interpretation of data gained by ecological and agricultural investigation, are generally developed in the course of experiments in which some element of exact laboratory control enters. Field research and laboratory research should be regarded as different means of attacking the same basic problems, not as separate branches of plant science.

METHODS OF CONTROLLED EXPERIMENTATION

The complete control of the environment of a plant in an experimental procedure is obviously beset with manifold technical difficulties, but it has been demonstrated that these difficulties may be overcome in sufficient degree to permit the realization of certain ideals of quantitative measurement, despite the complexity of the biological system. As an illustration, experiments conducted in this laboratory may be cited. Wheat plants were grown in chambers controlled with respect to light, temperature, humidity, air flow, and nutrient solution. In an earlier form of these chambers (Davis and Hoagland),[5*] control was available only within a limited range of conditions, but a more elaborate installation[†] makes feasible the accurate control of humidity and temperature over a wide range, illumination of regulated intensity and duration being supplied by Mazda lamps.

By the use of such chambers, experiments can be replicated at will, with a very small probable error. Therefore it becomes possible to compare with quantitative accuracy many known combinations of variables in successive experiments. Using a pure line seed, "standard" sets of plants may be grown at any time which are essentially identical, as judged not only by the superficial criteria of growth, but also by organic and inorganic composition, as has been shown recently by A. R. Davis[‡] and his coworkers.

It is, of course, recognized that there are formidable obstacles to the wide extension of this kind of experimentation. Chief among these obstacles is the practical difficulty of producing artificial light of suitable intensity and quality. The growth of many species of plants, under the kind of artificial illumination usually employed, is very different from that occurring under ordinary natural illumination. However, present difficulties are not insurmountable and there exists a rich field for exploration.

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[*] Superior figures refer to items in the bibliography at the end of this essay.

[†] This apparatus, erected by the Carriere Corporation, in consultation with Professor A. R. Davis and others, will be described later.

[‡] Unpublished data.

Although the artificial environment necessarily departs in many respects from any natural environment, certain general principles governing the response of the plant to its environment can be developed by laboratory research and may find an application in the study of plants in the field.

The solution of certain physiological problems requires the complete and accurate control of environment of the whole plant, but other problems, including most of those to be discussed in this paper, may be usefully studied for the present through methods of partial control, accomplished in the greenhouse or laboratory. Water and sand culture technique afford indispensable means of controlling the nutrient environment of the root. It is true that this technique has been employed by plant physiologists for many years, but only recently have some of the factors been properly recognized and controlled. The importance of root aëration and of certain chemical elements formerly considered unessential, may be mentioned. Partial control of the aërial environment serves effectively for certain purposes. Duration of illumination can be increased through the use of artificial light at night; the intensity and quality of the natural light can be regulated to some degree by the use of special light filters, or screens; partial control of humidity or of air movement can be accomplished in suitable glass chambers. Furthermore, accurately controlled experiments may be made with isolated tissues, such as storage organs or root systems, where the factor of illumination does not immediately enter.

These methods of quantitative control are capable of leading to an understanding of certain interrelations between the plant and its environment which cannot be gained from observations on plants growing under uncontrolled conditions. Quantitatively controlled experiments have an obviously broad significance to the student of plant physiology whether his interest lies in ecology, or agriculture, or in specific plant functions, such as transpiration, translocation, photosynthesis, respiration, or absorption of nutrients. Suitable control of environment and quantitative measurement of biochemical changes in plants subjected to this control offer a promise that plant physiology may develop in due course some of the attributes of an exact science, at least so far as the methods of exact science are at present applicable to biological systems of such great complexity.

It is proposed to analyze certain problems of the soil-plant system with reference to experiments conducted in accordance with the views just outlined. For the greater part the discussion will be based on data recently acquired by a group of investigators working in California.

NATURE OF THE PROCESS OF ACCUMULATION OF MINERAL SOLUTES BY PLANTS

It is now generally understood that absorbing plant cells possess the power of accumulating certain chemical elements derived from the nutrient medium, not merely by fixing these elements in organic combination, but also by storing them in vacuolar sap in inorganic form. This frequently implies a movement of solutes against a concentration gradient, and work must therefore be done by the cell in this process. Observations on Valonia,[9] Nitella,[6] and other plant cells supporting this conclusion have been discussed so often in recent years that no recital of the arguments need be presented at this time.

The conception of protoplasmic activities as indispensably related to the absorption and accumulation of essential or non-essential mineral solutes has been fundamentally advanced by the work of Steward[10] in his investigation of storage tissues. It was clearly shown that ability to absorb solutes against concentration gradients (accumulation) is dependent upon a state of intense cell metabolism, which is reflected in the processes of aërobic respiration. This does not mean, however, that carbon dioxide production is a direct measure of the power of accumulation; in fact, there is reason to suppose that certain other metabolic transformations not readily measurable, but reflected by the ability of cells to grow and divide (according to Berry and Steward[10]), may be more directly related than respiration, as determined by carbon dioxide production, to the process of absorption and accumulation of solutes. In any event, a suitable supply of oxygen is requisite to those activities which must be set in action before the cell can remove solutes from a dilute outer solution and transfer them to an inner solution of higher concentration. Furthermore, these metabolic processes must proceed at a certain minimal rate in order that the cell may retain solutes already accumulated in the sap. The applicability of these general principles to growth of plants in the soil has been demonstrated by extensive studies conducted in this laboratory in recent years on the nature of absorption and accumulation of mineral solutes by root cells. A new approach is offered to many problems of availability of nutrient elements.

Oxygen Requirement for Accumulation of Solutes by Root Cells

One out of many experiments will illustrate the indispensable requirement of oxygen for the process of accumulation of mineral solutes by root cells. In this experiment barley plants were grown in culture solution for three weeks and then the entire root systems were excised, a very large number of uniform plants being used. One set of excised roots was placed in an experimental solution containing potassium bromide* and potassium nitrate, with a rapid stream of air passing through the solution for 10 hours. Another set of roots was subjected to a similar solution, but nitrogen gas instead of air was passed through it. A third set of roots served for the study of initial composition. Roots were frozen and thawed, and sap expressed, concentrations of nitrate, potassium, and bromine being then determined, and conductivity of the sap also.

It is shown in figure 1 that very large increases in concentrations in the sap of the ions named above, accompanied by correlated increase in conductivity, occurred when air was passed through the solution in which the roots were immersed, but actual salt accumulation was not significant when nitrogen gas was substituted for air. The nitrogen gas contained a very small amount of oxygen as an impurity, apparently sufficient to prevent, over the brief experimental period, loss of solutes already accumulated by the root cells.

The conclusion from this and other experiments, in brief, is that metabolic activities of root cells requiring oxygen bring about the very rapid intake of electrolytes, so that there are built up in the cell sap far higher concentrations of the ions concerned than exist in the external solution. As already stated, work is done by the cell in the process of accumulation. Diverse types of living plant cells represented by storage organs, certain aquatic plants, and root systems of higher plants all seem to have the same general requirements for solute accumulation. The mechanism by which energy is used in the transport of solutes against concentration gradients is still without an explanation in accord with all experimental evidence.

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* Bromine is a very convenient element for studies on accumulation, and does not differ from the ordinary nutrient elements in its relation to the general physiological processes involved.

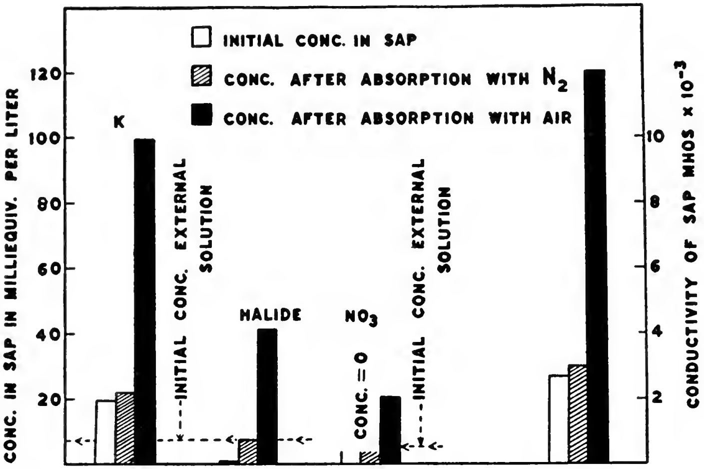

Fig. 1. Effect of aëration on accumulation of salt by excised roots of barley plants.

Each set of root systems represents 168 plants previously grown in a complete culture solution from May 31 to June 26. Absorption period, 10 hours; temperature of solution, 24° C.

$$\text{Experimental solution: } \left\{\begin{array}{ll} \text{KBr} & .0075\ \text{M} \\ \text{Ca(NO}_3)_2 & .0025\ \text{M} \end{array}\right\} 3000\ \text{cc.}$$

pH of culture: initial, 6.0; final, air 5.8; N_2, 6.3.

During the absorption period, a rapid stream of air was passed through one solution and purified nitrogen gas through the other. The nitrogen gas, however, retained traces of oxygen. Some oxygen was also present in the tissue and solution at the beginning of the absorption period.

It should be noted that much of the nitrate absorbed was reduced, and that potassium absorbed in association with nitrate remained in the sap in equilibrium with organic acid anion formed in the course of metabolism.

Numerous consequences arise from the principle that absorption and accumulation of mineral elements are dependent on protoplasmic activities. In the first place, the oxygen requirement of root cells and the oxygen-supplying power of the soil assume a new and specific significance. No matter what the concentration of solutes in the soil solution may be, these solutes are not physiologically available to the plant unless oxygen is supplied to the roots, and carbon dioxide removed, at the necessary rates.

Our general knowledge of the oxygen requirements of roots leads to the supposition that in this regard great differences exist among plants of different types. Investigations of this laboratory suggest that barley plants can maintain active accumulation of mineral solutes at relatively low oxygen tensions, considerably lower than that of the atmosphere. But similar oxygen tensions may be inadequate for certain plants, and some probably have oxygen requirements much lower than that of barley.

The supply of oxygen to the roots may not be derived exclusively from the soil atmosphere. Cannon[3] has concluded that translocation of oxygen from the leaves to the root system may occur during periods of photosynthetic activity. If this is an important source of oxygen for root activity, then illumination has a rôle in the absorption of mineral elements not previously suggested, and anatomical adaptations facilitating the transfer of oxygen assume significance in the study of the mineral nutrition of plants. The importance of this transfer would depend upon the physical structure of the soil, rainfall, activities of microörganisms, and all other factors which determine the power of the soil to supply oxygen to the roots.

In connection with root activities, the effects of carbon dioxide concentrations in the soil atmosphere are likewise of interest. Such concentrations may rise to relatively high levels at certain times. It has not been shown that absorption of mineral solutes is necessarily depressed by carbon dioxide concentrations likely to be present in the soil atmosphere, but the whole relation of carbon dioxide-bicarbonate equilibrium to root growth and solute absorption requires further careful study. It is obvious that the soil system is influenced not only by the metabolic activities of root cells, but also by those of soil microörganisms. The latter aspect of soil-plant interrelations, although it is of utmost importance, cannot be discussed in this brief review.

Energy Supply for Accumulation of Solutes

Since energy exchanges are involved in the processes of accumulation of solutes, a supply of available carbohydrate must be furnished to root cells and synthesis and translocation of sugars are therefore closely interrelated with mineral nutrition. Preliminary evidence is available that depletion of the supply of sugar or other available carbohydrate in the root system is accompanied by a retardation or inhibition of the absorption of mineral solutes and that feeding sugar to the roots, under otherwise suitable conditions, restores, at least in part, the accumulating power of the root cells, lost as a result of sugar depletion.

The mineral elements absorbed from the culture medium are, directly or indirectly, indispensable to the photosynthetic activities of green cells, and beneficent or vicious cycles in the soil-plant system may be established. For example, a limitation in the supplying power of a soil for potassium may lead to an impairment of leaf function (but not necessarily because potassium has a direct rôle in the process of photosynthesis) and consequently to a diminution in the rate of supply of carbohydrate to the root system. A retardation of root growth or metabolic activity may follow with a corresponding retardation of the rate of accumulation of potassium from the soil solution. A further starvation of the shoot for potassium ensues, and so the cycle proceeds, with a trend toward some sort of equilibrium between shoot and root. Injury or death of the plant may occur, however, before such an equilibrium is attained.

The amount of fruit or seed production, which is determined in part by climatic and biological factors, will affect the requirement of the plant for potassium or other nutrients and therefore affect estimates of the adequacy of soil conditions. Heavy fruiting will tend to diminish the amount of carbohydrate available for root activities, and, according to the views already presented, lessen the capacity of the root system for absorbing nutrients. The soil does not possess a fixed power for producing plant growth, but has instead a physiological value which cannot be adequately appraised without reference to the whole soil-plant system, and in relation to internal plant factors and to climatic environment. A basis for these statements has been established primarily through experiments with plants of agricultural interest, but the general principle is of wide application.

CERTAIN FACTORS OF THE CLIMATIC ENVIRONMENT AND ROOT GROWTH

Other interrelations of root and shoot exist which are much more obscure. In growing young barley plants in the greenhouse at different times of the year, under a given uniform nutrient supply, it has been observed that both the quantitative relation of root to shoot and the nature of the root system, as reflected by development of fine lateral roots, vary in a highly significant manner, depending on seasonal conditions. The relationship is illustrated in figure 2. The proportionate yield of roots is far higher in summer than in winter. Without discussing details of the experiments at this time, it may be said that not temperature, but some factor of illumination, seems to determine the extent and nature of the root system. It is not a question of ordinary photoperiodism, but of the quality or intensity of the light.

Recent investigations on plant hormones[1, 2] suggest that growth determinants of this type, the production of which de-

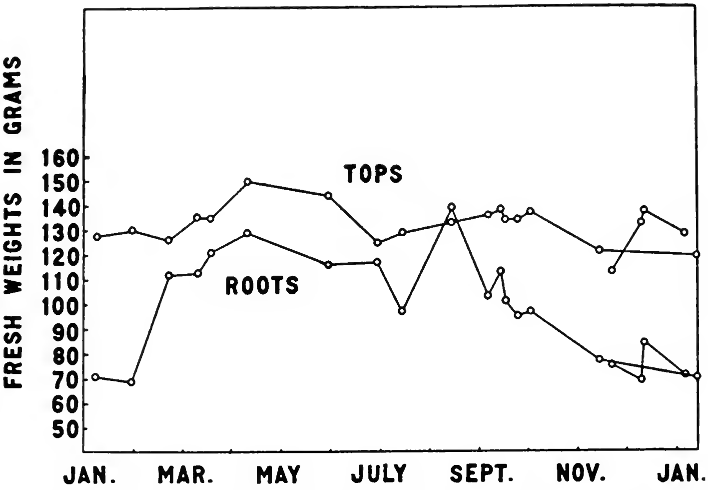

Fig. 2. Yields (fresh weights) of shoots and roots of barley plants grown in culture solution, in greenhouse, at different periods of the year; 168 plants grown in each set for periods of approximately 3 weeks. Roots, before weighing, were centrifuged by a uniform technique in order to remove adhering moisture.

Composition of culture solution:

$Ca(NO_3)_2$	.0025 M
KNO_3	.0025 M
$MgSO_4$	.001 M
KH_2PO_4	.0005 M

Fe added at intervals as iron tartrate.

pends on suitable illumination, may possibly cause the observed effects on root development. For the particular experiments now under discussion, a simpler explanation cannot at present be excluded, in terms of a supply of organic nutrients, synthesized when light of suitable intensity and quality is available, although it does not seem that the problem is one merely of carbohydrate supply. Whatever the mechanism may be, it is clear that a suggestion emerges for the study of a specific influence of the light factor on root growth and therefore on the relation of the plant to the soil.

TEMPERATURE INFLUENCES

The expectation is that the metabolic activities of root cells governing the accumulation of solutes should have a high temperature coefficient over certain ranges of temperature, and ample experimental evidence is now available to support this expectation. In barley roots, for example, the accumulation of mineral elements has a high temperature coefficient in the range 6° C.–24° C., but the rate of accumulation may increase with temperature up to 30° C., or higher, at least over a brief period of time. The lower temperature limit for accumulation has not yet been determined, but it is probably not far below 5°–6° C. It is, however, interesting that accumulation of mineral solutes can proceed slowly even at this low temperature.

A typical example of temperature influence on accumulation (for potassium) is given in figure 3. Barley plants were grown in nutrient solution for approximately three weeks and then the root systems were excised. These excised root systems were immersed in solutions of potassium salts and subjected to varying temperatures for limited periods of time, under conditions of aëration suitable for high respiratory activity. The temperature coefficients indicated are of a high order and in no way suggestive of simple diffusion processes. It is evident, rather, that temperature is influencing metabolic rates and that these are controlling the rate of accumulation of potassium. When the entire plant is studied, other complicating factors enter.

The results cited are not restricted to the barley plant. Very similar temperature relations have been observed in experiments with Nitella cells and storage tissues. The temperature coefficients for the accumulation of different elements are not necessarily identical, but it must be emphasized that temperature

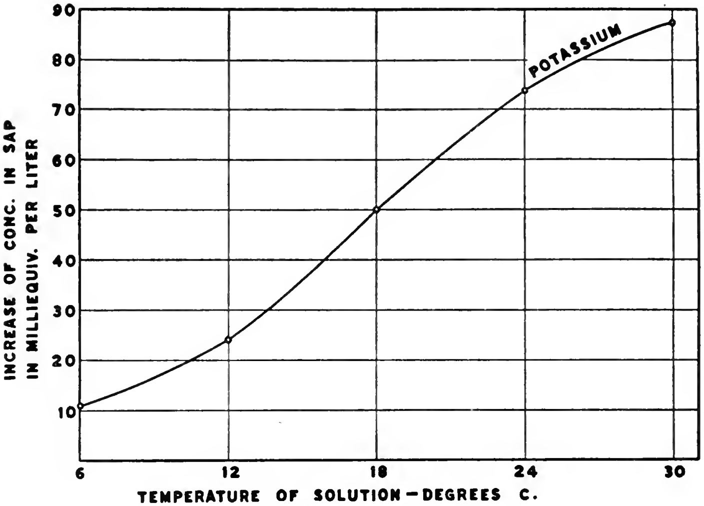

Fig. 3. Effects of temperature on accumulation of potassium in sap by excised barley root systems; each set represents 168 plants, previously grown in a complete culture solution for 21 days.

Absorption period, 10 hours.

Experimental solution:		
	KBr	.005 M
	KNO_3	.005 M
	$Ca(NO_3)_2$	.002 M

The temperatures of the solutions were maintained as shown within approximately plus or minus 0.2° C.

effects are not restricted to any special type of ion. The absorption of both anions and cations is influenced by temperature.

The importance of soil temperature with special reference to ecology or to practical agriculture is apparent. Seasonal and diurnal changes in soil temperature must influence enormously the rates of absorption of mineral solutes within certain ranges of temperature, and under conditions otherwise favorable to absorption. The general significance of this factor has been emphasized by Lundegårdh,[7] but as yet the relationship of soil temperature to mineral nutrition has received but scant general attention, and adequate data on temperature coefficients for plants of diverse types do not exist. It may be reasonably assumed that temperature limitation of mineral solute absorption sometimes constitutes a limiting factor for plant growth. And yet, high temperatures hasten depletion of carbohydrate reserves through accelerated respiration. When plant growth is being studied over an extended period, rate of photosynthesis and of translocation of carbohydrate to the root system, as well as rate of translocation of salts from root to shoot, should be considered in the evaluation of soil temperature effects.

HYDROGEN ION EFFECTS

Few factors in the plant's environment have received so much discussion as hydrogen ion concentration, but with each addition to our knowledge it becomes clearer that hydrogen ion concentration cannot profitably be interpreted in terms of an isolated variable. Leaving aside the well-known effects of hydrogen ion concentration on the solution of certain physiologically important chemical elements of the soil, there remains a highly complicated interrelationship between hydrogen ion concentration of the soil solution, buffering system of the soil, metabolism of the plant, and accumulation of mineral solutes.

Some of the recent studies of this and other laboratories lead to doubt whether, within a wide range of values, external hydrogen ion concentration *per se* is as important a factor as many investigators have believed. It is evident from data already available that the effects of hydrogen ion concentration must be reexamined with reference to root temperature, oxygen supply of the culture medium, and other factors controlling rates of root metabolism. The view now suggested is very different from that derived from the assumption that hydrogen ion concentration is mainly operative through some relatively simple physicochemical system which may be explained by reference to Donnan equilibria, protein isoelectric points, hydrogen ion gradients, and other factors of the kind.

Transpiration and Absorption of Mineral Solutes

The relation of the absorption and transpiration of water by plants to the absorption of mineral elements, or to their movement within the plant, has been discussed by plant physiologists decade after decade. Yet the most recently published articles reflect a striking diversity of opinion with respect to the function of transpiration in the economy of the plant—whether it is a necessary evil or is beneficial. There remains great uncertainty concerning many features of the movement of water and solutes within the plant's conducting systems, but several aspects of the absorption of mineral elements in relation to absorption and transpiration of water can be clarified on the basis of simple and convincing experiments.

Metabolically active root cells, when in a low salt condition, have the capacity to accumulate mineral solutes with great rapidity from a dilute solution, even when the root is severed from the shoot, as has already been demonstrated. Under suitable conditions and over a brief interval of time, almost as great a quantity of certain mineral solutes can be absorbed from a culture solution by the excised roots alone as by the whole plant. Transpiration is therefore not involved in the first step of the process by which plants remove solutes from the soil.

The plant as a whole being considered, root cells, when in a state of high metabolic activity and not already saturated with mineral solutes, may absorb some ions from the culture solution

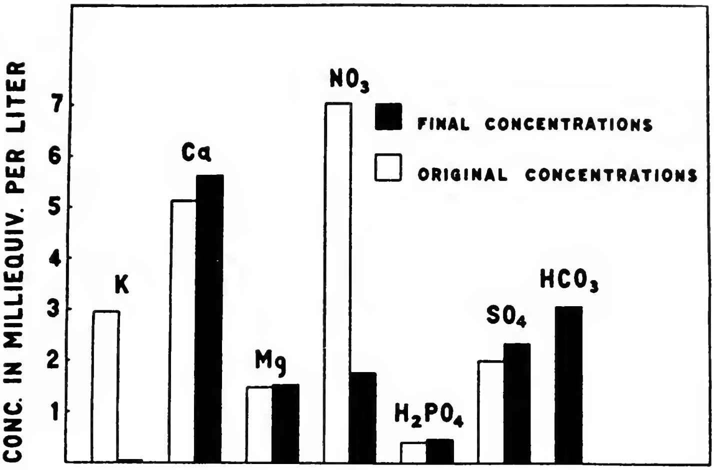

Fig. 4. Relation of water and solute absorption; barley plants (duplicate sets of 168) grown for 19 days in a complete culture solution.

Experimental period of absorption, 24 hours.

Solutions used, same as described under figure 2.

Correction made for very slight loss of water caused by evaporation from solution; 825 cc. of water absorbed by each set of plants, from original volume of 3900 cc.

Each set of plants absorbed the following total quantities of the various ions (in milligram equivalents):

K	11.5	NO_3	22.0
Ca	2.6	SO_4	0.6
Mg	1.5	H_2PO_4	0.2

HCO_3 determined by titration method. Some organic acid radicles may have been present.

at a proportionally much faster rate than water and as a necessary consequence the nutrient solution becomes diluted with respect to these elements. A recent experiment (fig. 4) illustrates this point. The roots of young barley plants were immersed in an aërated nutrient solution for twenty-four hours, without any addition of water. The arrangements permitted only a very slight amount of water to escape by direct evaporation from the solution. At the end of the period, the residual solution was analyzed and compared with the original solution.

The concentrations of potassium and nitrate were greatly reduced, potassium almost to zero, while calcium, magnesium, and sulphate ions were present in the residual solutions in slightly higher concentrations than in the original solution. Obviously, solutes were absorbed much more rapidly than water with respect to the first concentrations mentioned. Furthermore, the general balance of ions was completely changed by the absorptive processes of the plant. Bicarbonate ions, present at the beginning in only negligible concentration, entered or were formed in the culture solution in large concentration as a result of those root activities which brought about a larger intake of anions than of cations. The metabolic activities of the root system, through their relation to the absorption of mineral solutes, thus effectively and continuously disturb the equilibrium conditions of the solid and solution phases of the soil.

The conclusion has been generally accepted in recent years by plant physiologists that absorption of mineral solutes is independent of transpiration, but much of the earlier evidence for this conclusion (growing plants in shade and sunlight, and determining ash content, and the like) has not permitted the same unambiguous interpretation as may be placed on the results from simpler experiments of the type referred to just above. A satisfactory understanding of the phenomena requires an appreciation of the rôle of root metabolism in accumulation of mineral solutes from dilute solutions. Although the independence of the processes of transpiration and of mineral solute absorption is established, it has not been proved that transpiration does not indirectly influence absorption of solutes over an extended period. A certain upper limit of concentration exists for root cells, no matter how intense their metabolism, and the continuance of absorption from a nutrient solution depends upon movement of solutes from the root to the shoot.

This raises once more the question of the path of translocation of mineral solutes. Doubtless, most investigators in the field of botany feel that the assumption may be safely made that these solutes are always moved upward in the transpiration stream, but this assumption is not accepted by all investigators. Curtis[4] has presented evidence with respect to woody plants which indicates very strongly, he thinks, that movement occurs primarily in the living cells of the phloem and not in the xylem system. Experiments with certain annual plants, however, lead to the conclusion that movements of inorganic solutes of large magnitude do occur in the xylem system, and this may be the chief, possibly the sole, path of conduction in the plants concerned. If so, transpiration would have a function in the removal of solutes from the root system and would therefore influence the efficiency of root activities in the process of absorption of mineral solutes. Whatever may be the path or the mechanism of translocation, growth and metabolism must be concerned in the accumulation or utilization of mineral solutes in green cells just as in root cells. The distribution of mineral elements in different tissues cannot be explained without reference to the metabolic activities of living cells, in relation to solute accumulation, and to the effects of climatic environment upon these activities.

With respect to another aspect of translocation, it has been demonstrated that a very direct relationship frequently exists between root pressure and rate of accumulation of mineral elements from solution.* The rapid accumulation of electrolytes by the root system establishes an osmotic gradient resulting in

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* Unpublished data by D. R. Hoagland and T. C. Broyer.

exudation from cut surfaces or in guttation, under appropriate atmospheric conditions. The guttation water, and especially the exuded sap, from cut stems, may contain certain solutes in much higher concentrations than those of the culture solution. Upward movement of mineral solutes can therefore occur under the influence of the forces of root pressure, closely related to the metabolic activities of root cells. The results of some recent experiments suggest that such solutes enter into the xylem system by a polarized process involving metabolic activities of root cells.

Soil and Plant Interrelations

Having surveyed in a general way the nature of the process of absorption of mineral elements by plants, we must now give some further consideration to certain interpretations in terms of soil-plant relations, without, however, discussing the chemical and physical system of the soil—a subject of extreme complexity.

The plant is generally compelled, by virtue of the properties of the soil environment, to remove essential mineral elements from dilute solutions. Some of the essential elements will ordinarily be present in the soil solution in extremely low concentrations. It is necessary for the rapidly growing plant to acquire certain of these elements at rates which are extremely high in comparison with those of the concentrations available. The plant does in fact function as an active concentrating agent. (Its remarkable efficiency in this respect has been referred to earlier.) Active root growth also constantly brings into play new soil surfaces which yield solutes to the plant, and this exploration of the soil is likewise dependent upon metabolic activities of the whole plant. These considerations apply not only to the essential elements of older history, but also to other essential elements only recently recognized as essential, such as boron, copper, and zinc.

The respiration of root cells, an activity which must proceed in order that accumulation of solutes may take place, is also a source of hydrogen ions, which can bring about the solution of bases or of other elements from the solid phase of the soil. Great importance thus is assigned to the displacement by hydrogen ions of calcium, magnesium, and potassium from those colloidal complexes of the soil in which the properties of base exchange chiefly reside. In this displacement we find a very direct relation between metabolic activities of root cells (also, therefore, an indirect relation with activities of leaf cells) and the dissolving of certain essential elements from the solid components of the soil system. There are thus two important general consequences of root metabolism as related to nutrition with respect to cations —production of hydrogen ions, and disturbance of equilibrium through absorption of bases by root cells. The latter process is of course selective, potassium ions being withdrawn usually at a far greater rate than calcium or magnesium ions.

Among the anions absorbed by plants, nitrate is ordinarily of greatest quantitative importance and this ion has a special significance for soil-plant interrelations as determined by metabolic activities of the plant. The nitrate is often removed from solution in excess of bases, leaving bicarbonate or organic acid ions derived from the tissue in concentration equivalent to that of the excess nitrate removed. In effect, an exchange of ions occurs.

Nitrate ions may be removed from solution and concurrently undergo reduction, or they may be accumulated in the cell sap as nitrate ions and subsequently reduced. Recent experiments on barley plants indicate that the accumulation of nitrate ions as such is controlled by the same metabolic activities that control accumulation of other ions. As conditions become less favorable for aërobic processes, the removal of nitrate ions from solution (as differentiated from accumulation of nitrate ions in the cell sap) may be less affected than the removal of other ions, the reason apparently being that the absorption of nitrate accompanied by reduction does not depend upon an oxygen supply in the same way that the accumulation of nitrate and other ions does. Accordingly, the extent of the selective removal of nitrate may be a function, not merely of the character of this ion, and of the associated basic ions, but also of the kind of metabolism occurring in root cells.* Furthermore, the experiments of Lundegårdh and Burström,[8] and of investigators in California, show that respiration may be accelerated in the process of absorption of certain ions; particularly the nitrate ion, as results obtained in this laboratory make plain. This again illustrates the complexity of the reciprocal relations existing between the soil and the plant.

In the accumulation of mineral elements by root cells, interionic relations play an important rôle. It has been more than sufficiently shown that these relations are not limited to strong solutions, nor to interrelations of cations. The explanation of the results cannot be given satisfactorily in terms of a simple physicochemical system, for the reason that we are dealing with a dynamic system in which the nature of many of the metabolic reactions is still unknown. Interionic effects, nutrient deficiencies, and the relative rates of absorption of ions of varied character should be reinvestigated with reference to oxygen and available carbohydrate supply to the root system, temperature of soil, and related factors. Such an investigation must form a part of any comprehensive plan of attack on the nature of soil-plant interrelations.

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* The activities of microörganisms living on root tissues require additional study, but at present the metabolism of the root cells seems to be primarily concerned.

ACCUMULATION OF MINERAL SOLUTES AND PLANT BUFFER SYSTEMS

It is beyond the scope of this contribution to enter into a general discussion of the function of mineral elements in plant growth, but some comment on the mineral nutrition of the plant in relation to the buffer system of the cell sap is useful, as illustrating another problem of soil-plant systems.

There is a fundamental difficulty in the quantitative examination of the buffer systems of complex plant tissues in that some method of expressing sap from such tissues must be employed and the resultant fluid is a composite and to some extent altered sap. Nevertheless, important information has been gained. The tendency to maintain specific hydrogen ion concentrations, within a rather narrow range, is very marked in many plant tissues, as can be observed even under the highly imperfect conditions of present experimentation. Phosphates and salts of organic acids are of especial importance in most plant buffer systems. The metabolic activities of the cell determine, on the one hand, the accumulation of the mineral components of the buffer system, and on the other hand, the transformations of organic substances to provide organic acid radicles. Oxygen and available carbohydrate supply, temperature, and other factors already discussed, are essentially concerned in both aspects of the processes which operate to maintain a suitable buffering system in the sap.

The predominate anion capable of ready metabolic transformation is the nitrate ion. Nitrate and bases enter the plant and nitrate undergoes more or less rapid reduction followed by the synthesis of organic forms of nitrogen. A basic residue is left and this is neutralized by organic acids.

The nature of the mineral and organic complexes of the soil determines the inherent supplying power of the soil for basic and acidic ions, but the metabolic activities of the plant govern the rates at which absorption can occur. The maintenance of suitable internal hydrogen ion concentrations in plant tissues is dependent on the proper functioning of the system as a whole. The measurement merely of the reaction of the external solution gives but a very faint insight into the rôle of hydrogen ion concentration in plant growth, and undue simplification of the problem may readily lead to fallacious conclusions.

GENERAL CONCLUSIONS

This survey is very incomplete, yet it is believed that the evidence presented by way of illustration suffices to establish the general thesis proposed in the Introduction. Many problems of the soil-plant system can be reoriented if the view be adopted that the plant not only occupies the soil, but also constitutes a metabolic unit in the whole environment, aërial and subterranean.

This is not a vague and sterile generalization, but on the contrary, one which leads to specific and fruitful suggestions for future experimentation. The soil is regarded as a medium which must provide a suitable environment for root metabolism. Soil temperature and aëration assume a definite importance in the study of solute absorption. More specific reasons than have been apparent heretofore are found for investigating the relation of leaf metabolism and of the demands of reproductive processes to the metabolism of root cells. The indirect effects of the quality, intensity, and duration of light on root development are recognized as requiring far more intensive study than has yet been accorded to them. Transpiration becomes of interest in relation to changes in the concentration of solutes in the soil solution and to the aëration of the soil. Transpiration or other factors influencing rate of movement of mineral solutes out of the root system indirectly modify the rate of intake from the soil solution and the problem of translocation requires investigation with this in mind. There is need of further knowledge of carbon dioxide production by root cells, as influenced by soil aëration, soil temperature, carbohydrate synthesis and translocation, and related factors.

The discussion may be appropriately closed by emphasizing again the general view that problems of the soil-plant system cannot be solved without the aid of patient and laborious experimentation under conditions which permit the requisite control of the plant's environment and the quantitative measurement of processes or of their end products. Such researches are indispensable to the development of scientific knowledge in the field of geobotany or of practical agriculture.

SUMMARY

The metabolic activities of the plant are reviewed with special reference to the absorption of mineral elements. Methods of controlled experimentation are considered and certain results cited. In connection with the process of solute accumulation, emphasis is placed on the supply of carbohydrates available to root cells, and on the temperature and oxygen-supplying power of the root medium. Relations of transpiration to absorption of mineral solutes, relation of absorption of these solutes to plant buffer systems, and other interrelations of the soil-plant system are discussed.

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Malaysian Phytogeography in Relation to the Polynesian Flora

By E. D. Merrill

In any general treatment of the flora of Polynesia, whether this be merely a taxonomic consideration or a discussion of the phytogeography of the region and the relationships of the flora to that of surrounding lands, it is manifest that the vegetation of the islands that form the western boundary of the Pacific is a major factor to be considered. At the present time, representatives of between 1400 and 1500 more or less generally recognized genera of flowering plants and ferns are known from Polynesia. However, this estimate includes New Caledonia, which is remarkable for its very specialized flora, and comprises the very numerous exotics introduced by man. More than 1100 of these genera occur also in Malaysia.

Essentially, the flora of Polynesia, whether we consider that of the low or the high islands, is Malaysian in origin, with certain characteristic Australian elements which also occur in Malaysia and particularly in Hawaii, with a small admixture of American forms. No single family of plants is confined to Polynesia, and the number of endemic genera is relatively small. Specific endemism in the low islands is very limited, most of the species being those of wide tropical distribution. With the exception of the weeds and cultivated plants introduced directly or indirectly by man, the flora of the low islands is chiefly composed of species having special adaptation for dissemination by ocean currents. However, in each of the groups of high islands in Polynesia there is a distinctly high specific endemism, which is in general true of oceanic islands, but the relationships of these endemics are in large part with the genera and species characteristic of the tropical lands bordering the western Pacific. The purpose of this paper is not to theorize concerning how or when these various types, or their ancestors, reached Polynesia, but rather to point out certain obvious facts in present-day distribution and briefly to discuss the bearing that our limited knowledge of the geological history of the Malaysian region has on this problem.

The so-called monsoon region in the Asiatic tropics has its typical flora, and no sharp distinction may be drawn between that of tropical Asia and that of the great archipelago that lies between Asia and Australia. Whether many of the genera characteristic of this region originated in what is now continental Asia and migrated into Malaysia, or vice versa, is a question that can scarcely be settled definitely and is perhaps of slight importance; unquestionably there have been extensive intermigrations in both directions. We do know, however, that there are a number of characteristic Asiatic (continental) types in Malaysia, occurring at both low and high altitudes, and that these types, as a rule, do not reach Polynesia. Some of the numerous Asiatic genera having indigenous representatives in Malaysia are: *Taxus, Pinus, Agrostis, Anthoxanthum, Bromus, Deschampsia, Muhlenbergia, Poa, Asparagus, Lilium, Ophiopogon, Salix, Ulmus, Arenaria, Anemone, Ranunculus, Thalictrum, Sedum, Astilbe, Deutzia, Sycopsis, Photinia, Rosa, Gleditschia, Skimmia, Buxus, Sarcococca, Pistacia, Berchemia, Hypericum, Viola, Daphne, Acanthopanax, Sanicula, Primula, Lysimachia, Fraxinus, Ligustrum, Acer, Gentiana, Sweertia, Trigonotis, Vaccinium, Rhododendron, Gaultheria, Ajuga, Mosla, Salvia, Alectra, Bythophytum, Hemiphragma, Sopubia, Lonicera, Peracarpa, Ainsliaea, Anaphalis, Aster, Cirsium, Lactuca,* and *Solidago.* There are many others both at low and at high altitudes.

The intermigrations of the early angiosperms in what is now tropical Asia and Malaysia doubtless took place at a time when the continental area extended far to the south, probably in the late Cretaceous and early Tertiary, and this is the period when the more widely dispersed Asiatic types, or the ancestors of certain Asiatic types now found in New Guinea, extended their ranges. There seems to be little or no evidence of direct Asia-New Guinea land connections since the early Tertiary.

The evidence is that, in later times, there were an eastern and a western route of intermigration as between Asia and Malaysia, the former from southeastern Asia and Formosa south through the Philippines at least as far as Celebes, and the latter from India through Burma and the Malay Peninsula to Java, Sumatra, and Borneo, with apparently a secondary paralleling line through what is now the Andaman Islands to Sumatra and perhaps Java. These routes were doubtless in operation at a relatively early time, probably in the Tertiary, so far as the ancestors of our modern flora were concerned. At a later period, particularly from the Pliocene-Pleistocene into the Recent, there must have been a very active interchange of plants between Asia and western Malaysia, when the Sunda Islands (Java, Sumatra, and Borneo) and the Palawan-Calamian group in the Philippines were at times definitely a part of the Asiatic continent.

The Malay Archipelago lies wholly within the tropics. This great equatorial group of islands extends from the northwest to the southeast, from northern Sumatra to eastern New Guinea, a distance of about 4000 miles. Throughout this vast region the climatic conditions are essentially uniform; for the most part, precipitation is ample and, in certain areas, even extreme, and the average temperatures at equal altitudes are strikingly uniform. In the Malay Peninsula, Sumatra, Java, Borneo, the larger islands of the Philippines, Celebes, the Moluccas, and New Guinea, there are numerous mountains from 5000 to 8000 feet high, with peaks at least 10,000 feet high in Sumatra, Java, Celebes, Luzon, and Mindanao. The maximum elevations are 13,700 feet in Borneo and about 16,000 feet in New Guinea. These high mountains form "islands" within the tropics where, once established, species adapted to temperate and subtemperate conditions have persisted. Certain parts of the archipelago have prolonged alternating wet and dry seasons in each year, and others have a rather uniform distribution of rainfall in all months of the year. In the great islands, there are no regions that approach arid or even semiarid conditions, and there is perhaps only one part of the entire region where the restricted annual rainfall appreciably affects the vegetation. This part comprises some of the Lesser Sunda Islands. The rainfall—its amount and its seasonal distribution—is the most important single factor, aside from altitude, which affects the distribution of vegetative types in all Malaysia. At low altitudes, the remarkably uniform temperature has had little limiting influence on the distribution of plants. The prevailing winds, which affect vast areas for several months each year, are of minor importance to vegetative types except as they affect the seasonal distribution of rainfall. There are no striking differences in soil types except in limited areas. Therefore, neither precipitation, humidity, temperature, nor soil conditions can cause the vegetation of any major part of the Archipelago to be strikingly different from that of any other major part at a similar altitude.

Yet there are remarkable differences in dominant families, genera, and species between the known flora of any two great islands, or contiguous groups of islands, particularly between eastern and western Malaysia. It is true that most of the families of plants having native representatives in Malaysia are generally distributed throughout Insulind, and the same is true of many of the dominant genera. Yet certain families, such as the Dipterocarpaceae,* that dominate the primary forests of western Malaysia, become distinctly unimportant in eastern Malaysia, and, conversely, a considerable number of genera of the Myrtaceae that occur in eastern Malaysia, fail to reach western Malaysia. Some of these genera are *Eucalyptus, Mearnsia, Xanthostemon, Osbornia,* and *Xanthomyrtus* (the last two also are found in Borneo). Furthermore, there is a remarkable development of specific endemism; every large, medium-sized, and even small island in the group has a very high percentage of species that, so far as we know at present, are found only on that island, or on a certain part of it, or on a restricted group of neighboring islands. Had there not been some active limiting factor, there is no evident reason why a great many of these thousands of local species should not now have more general geographic distribution, or why certain families and genera should be dominant in or limited to specific parts of the Archipelago. This limiting factor seems to be found in the geologic history of Malaysia. From the Tertiary, a more or less continuous insular area existed in some part of this region, the straits and arms of the sea inhibiting the natural dispersal of a great many species of plants and animals.

We know little about the climatic conditions of Malaysia in past geologic times, but we may deduce from the present-day vegetation that for a long time the climate has not been strikingly different from that which obtains today. Certainly there have been no periods in which the low-altitude vegetation was affected

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* Merrill, E. D., 1923. Distribution of the Dipterocarpaceae. Origin and relationships of the Philippine flora and causes of the differences between the floras of eastern and western Malaysia. Philip. Jour. Sci., 23:1–33, *t. 1–8.*

by cold weather, and no extensive areas in which arid or semi-arid conditions prevailed. In other words, since the beginning of the development of our modern vegetation, Malaysia as a whole apparently has been a continuously tropical region with a remarkably equable climate, ample rainfall, and relatively high humidity. From the limited paleobotanic record, we know this has been true of certain parts of the region in which the Pliocene-Pleistocene plant-remains perfectly match the plants of today, but we can only surmise that this is true for the entire region. Setchell* has suggested that persistently dry areas, or the alternating wet and dry seasons characteristic of certain parts of the Archipelago, may be just as important to plant distribution as the geologic history of the region, a suggestion that cannot be ignored; yet it is significant that we find throughout Malaysia, more or less in alternation, constantly wet and alternatingly wet and dry regions; for example, western Java is contrasted to eastern Java, and all the east coast of the Philippines to the west coast. Even in regions dominated by alternating wet and dry seasons there are found certain areas, particularly in the vicinity of high mountains, where precipitation is more or less equably distributed through all months of the year; such areas occur on almost every island in Malaysia which has mountains 4000 to 5000 feet high or higher.

It has been known for many years that the fauna of the Sunda Islands is essentially Asiatic, and that as one proceeds eastward the Asiatic mammals, fresh-water fishes, and certain groups of birds, reptiles, and insects become less and less evident. On the contrary, there are various striking Australian types of insects, birds, and other animals in New Guinea and neighboring

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* Setchell, W. A., 1929. The Wallace and Weber Lines: a suggestion as to climatic boundaries. Proc. Fourth Pacific Sci. Congr., 3:311–321.

islands. In general, this same statement applies to the plants. Mere proximity to Asia or Australia is, in part, the cause of this condition, but a brief consideration of geologic history will provide a fuller explanation.

The Tertiary was the period of the development and dissemination of mammals. The mammals were very poorly represented in Australia, where their place was taken by the more primitive marsupials. It seems evident that, in earlier geologic times, Australia was definitely united with Asia, but was separated from it before the mammals became dominant. This in part explains the plant and animal forms, long-continued isolation favoring local development uninfluenced by direct migrants from Asia. In pre-Tertiary times, intermigration was possible until the late Cretaceous; since that time most northwestern-southeastern intermigrations have been inhibited by the constant archipelagic conditions of certain parts of Malaysia, and since the late Cretaceous or early Tertiary there apparently have been no direct land-connections between Asia and Australia. In the Tertiary, there were great physical changes in a large part of Malaysia, as is evidenced by the greatly developed Tertiary sediments in the Archipelago, but always, somewhere, there were apparently large land areas in existence.

Molengraaff has clearly indicated the probable geologic history of this region since the Tertiary.* There have been two fairly stable continental areas and an intermediate unstable insular area. The Asiatic bank, or Sunda shelf, extending southward from Asia, comprising approximately 1,850,000 square kilometers, carries upon it the Malay Peninsula, Sumatra, Java, and the smaller islands eastward to Bali, Borneo, and the Palawan-

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* Molengraaff, G. A. F., 1921. Modern deep-sea research in the East Indian Archipelago. Geogr. Jour., 57:95–121. *f. 1–9.* map.

Calamian group in the Philippines. In its fauna and flora this entire region is essentially Asiatic or, we might say, Malay-Asiatic. Marked by the 200-meter isobath, the eastern boundary of this shelf is, in its southern part, the famous Wallace's Line, so named by Huxley, supposedly demarking the limits of the Asiatic and the Australian faunas and a part of the eastern boundary of the ancient Malay-Asiatic continent, or Sundaland.

The Australian bank, or Sahul shelf, much smaller than the Asiatic one but having practically the same history, carries upon it the great island of New Guinea. The western boundary of this ancient continent, or Papualand, approximates the position of Weber's Line, proposed by Pelseneer as a substitute for Wallace's.

The insular area between Wallace's and Weber's Lines, including the Lesser Sunda Islands, the Moluccas, Gilolo, Celebes, and all the Philippines except the Palawan-Calamian group, has had an entirely different history. All or part of this intermediate region has been insular since the beginning of the Tertiary. There are no large shelf seas; on the contrary, the straits and seas between the various islands are marked by great deeps. This entire region has been subject to several great elevations and depressions. It has been and still is unstable, and, in contrast to the more stable Sundaland to the west and Papualand to the southeast, it is orogenetically active. Its flora and fauna are made up in part of relic species and their descendants, and in part of infiltrations from the west, north, and southeast. East of Sumatra, Java, and Borneo, Asiatic types sharply decrease; many do not extend to this intermediate area, and still more do not reach New Guinea. West of New Guinea, the Australian types decrease and most of them do not reach Sundaland, although a striking series has attained a northward distribution into the more distant Philippines.

In relation to Polynesia, it is naturally the eastern part of Malaysia that is of the greatest biological interest, for it is from this region that most of the Malaysian types of plants now found in Polynesia have been derived. There has been in Polynesia a certain amount of dissemination of plants by water, but the number of species having adaptations to this end is very limited. Other plants have been disseminated through the medium of winds and migratory birds. There are, however, many genera characteristic of Malaysia-Polynesia that have no manifest adaptations for any of these methods of dissemination. One is forced to postulate a different distribution of land areas at some time in the past, to explain the present-day distribution of plants and animals. These land areas probably were of considerable size, not the narrow land-bridges which have been widely scattered over the Pacific basin by some theorists.

Effective north and south distribution is limited by temperature, but within the humid tropics this factor is inoperative. Thus, except for a very few high-altitude plants in Luzon, there is no evident connection between the Philippine and the Japanese floras. Even the species distributed between Formosa and the Philippines are few in number and none is dominant in either region; and, strikingly, none of the characteristic Papuan and eastern Australian types, so well developed on the Philippines, reaches Formosa.*

The north and south distribution in eastern Malaysia is more extensive than is generally realized. Such characteristic species as *Uncinia rupestris* Raoul and *Blechnum fraseri* Luerss., originally known only in New Zealand, now stand thus: the *Uncinia,* New Zealand and the Philippines; the *Blechnum,* New Zealand,

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* Merrill, E. D., 1923. Die pflanzengeographische Scheidung von Formosa und den Philippinen. Bot. Jahrb., 58:599–604.

the Philippines, and Borneo. Among genera, about eight species of *Ascarina* are distributed in New Zealand, New Caledonia, and western Polynesia, and two species in the Philippines; about twenty-three species of *Quintinia* in New Zealand, New Caledonia, Australia, and New Guinea, and one in the Philippines; about ten species of *Mooria* (*Cloëzia*) in New Caledonia and one in the Philippines; about twelve species of *Xanthostemon* in New Caledonia, three in Australia, two in New Guinea, one in Celebes, and three in the Philippines; three species of *Phyllocladus* in New Zealand, one in Tasmania, and one in the Philippines and northeastern Borneo. Numerous eastern Australian types extend into eastern Malaysia as far north as the Philippines, including representatives of such diverse genera as *Centrolepis, Thysanotus, Patersonia, Phrygilanthus, Drimys, Clianthus, Pleiogynium* (also in Fiji and Vavau), *Stackhousia, Camptostemon, Eucalyptus, Osbornia, Pimelea, Xanthostemon, Calogyne, Microlaena, Didiscus,* and others, with a few more widely distributed. Such eastern Malaysian-Philippine genera as *Spiraeopsis, Wallaceodendron, Reinwardtiodendron, Neotrewia, Strophioblachia, Myrmephytum, Sararanga, Heterospathe, Pothoidium, Monophrynium, Papualthia, Cubilia, Euphorianthus, Tristira, Schuurmansia, Everettia, Mearnsia, Anompanax, Dimorphanthera, Loheria,* and *Nycticalos* range from the Philippines to Celebes and the Moluccas, and some to New Guinea.

It is significant that, although all these genera have species that are more or less widely distributed in the Philippines, few extend to western Malaysia and still fewer to the Asiatic continent. Among those that have the more extended range are: *Drimys* (Borneo), *Centrolepis* (Borneo and Indo-China), *Thysanotus* (Malay Peninsula, Indo-China, and China), *Clianthus* (Indo-China and Hainan), *Stackhousia* (Sumatra and Caroline

Islands), *Calogyne* (China), *Osbornia* (Borneo), *Didiscus* (Borneo), and *Strophioblachia* (Indo-China). No representative of any of these genera reaches Formosa, yet most of them extend to northern Luzon and some even into the Batan and Babuyan Islands, between Luzon and Formosa.

In general, the eastern Malaysian types have not extended north of the Philippines, and their western migration also stopped there, as the eastern migration of many western Malaysian types ceased in Borneo, the Palawan-Calamian group in the Philippines, and the Philippines proper.

This is entirely in accord with the supposed geologic history of the Malaysian region. The constantly insular area in the unstable region lying between the Lombok Passage and Macassar Strait, extending north along the western boundary of the Philippines to the west and east to the islands off the western end of New Guinea, including the Lesser Sunda Islands, Celebes, the Moluccas, Gilolo, and all the Philippines except the Palawan-Calamian group, effectively inhibited a general east and west migration across this region, not only in the Recent and the Pleistocene, but also during the Pliocene and probably some of the Tertiary. Undoubtedly there was some late east and west distribution across the southern part of this unstable insular area but, in general, the routes of migration seem to have been northeast from Sumatra, Java, and Borneo into the Philippines, and thence south and southeast to Celebes, Gilolo, and New Guinea, and vice versa. The species that succeeded in extending their ranges apparently were forced to travel along the two longer sides of a triangle, its base approximately in the position of the Lesser Sunda Islands and its apex somewhere in Luzon.

When a genus is described from material collected in a certain place and is known only from that region for many years, we more or less automatically accept it as a group characteristic of that region. If a representative of it is later found in another area, we are apt to consider it as an extraneous entity there. *Eucalyptus* is such a genus. It is tremendously developed in Australia, has a very few species in New Guinea, and one which extends to the Bismarck Archipelago, the Moluccas, Celebes, and the Philippines. We are justified in accepting it as an Australian element in the other regions. The same is true of the few phyllodinous species of *Acacia* outside of Australia. The one native species of *Ulmus* in northern Sumatra, two species of *Pinus* in Sumatra and the Philippines, and one species each of *Taxus* and *Gleditschia* in the Philippines and Celebes may be unquestionably accepted as Asiatic (continental) types in Malaysia. But consider the following genera:

The genus *Vavaea* was described in 1846 for a single species from Vavau in the Tonga Islands. When the first Philippine species was found, it was considered to be a Polynesian element in the Philippine flora; and yet seven species are now known in the Philippines, one in Java, three in New Guinea, one in the Caroline Islands, and still only three in Polynesia. This supposed Polynesian element in the Philippines and Malaysia is really a Malaysian element in Polynesia. *Couthovia* was even more mistakenly located. This genus was proposed in 1858 for two species, one from Hawaii and one from Fiji. In 1888 a third species was described from New Guinea, and ten years later a fourth from Celebes which, four years after, was found in the Philippines. Thus we had a "Polynesian" element in the New Guinea-Philippine-Celebes flora until the New Guinea flora became better known. Eleven species of *Couthovia* are now known from New Guinea and two from the Caroline Islands. *Couthovia* thus resolves itself into a Papuan genus which has extended its range north into the Caroline Islands (two species), southeast to New Caledonia (one species), east in Polynesia to Fiji and Hawaii (two species), and northwest into Celebes and the Philippines (one species). *Dolicholobium* was described in 1860 from Fiji. At present five species of it are known in Fiji, eight in New Guinea, one in the Solomon Islands, and one in the Philippines. Like *Vavaea* and *Couthovia,* this genus seems to be not so much a "Polynesian" as a Papuan type which apparently has extended its range north from New Guinea into the Philippines, as well as east into Polynesia.

May not such genera as *Joinvillea* and *Tetraplasandra,* for a long time known only from Polynesia, have the same history? The first is now also known from the Malay Peninsula, Sumatra, Borneo, and the Philippines, and the second from the Philippines and Celebes. As our knowledge of the tremendously rich and really not well-known Malaysian flora increases, we may expect to find, particularly in eastern Malaysia, various other generic types now considered to be Polynesian.

Future investigations may radically modify our beliefs concerning the geologic history of this region, but in general the present-day distribution of both plants and animals is in support of the geologic history as it is now understood. There is no sharp line separating the floras and faunas of eastern and western Malaysia nor those of Asia and Australia, except for limited groups; all proposed lines break down more or less when all groups of plants and animals are considered. Apparently both eastern and western Malaysian elements have introduced into the unstable insular area separating the more stable Sundaland and Papualand, which is what logically would be expected when an insular group is situated between two continental areas and the islands are separated by relatively narrow arms of the sea.

It may be that Wegener's hypothesis of continental shift has its bearing on both the separation and the intermingling of the Australian and Asiatic faunas and floras in Malaysia, if it be assumed that Australia, formerly more widely separated from Asia, moved toward Asia and, in so doing, crushed the southeastern borders of an ancient, larger Asiatic continent. Before the shift took place, intermigrations were impossible; after the shift, plants and animals could move to a limited degree in both directions. This hypothesis has been applied to the problem of plant distribution in Malaysia by Doctor Lam.*

We can only theorize concerning the underlying causes for the peculiar distribution of Australian types, which extend into Polynesia and eastern Malaysia, including the Philippines, but do not reach to any marked degree into western Malaysia. Our knowledge of the tremendously developed Malaysian flora and fauna is limited, and any conclusions based on the data now available concerning the distribution of known genera and species may be radically modified as exploration progresses and the compilation of geographic distribution data becomes more complete. Conclusions based on the known distribution of any one group, be it genus, family, or any other category, are notoriously unsafe. Conclusive generalizations can be safely based only on the consideration of all groups, and here the specialist fails because of his inability to master and evaluate the details of geographic distribution of organisms outside of his own special field.

It is safe to assume, however, that, whatever have been the causes leading to the present-day distribution of Malaysian life, no investigator of the fauna and flora of Polynesia can safely

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* Lam, H. J., 1930. Het genetisch-plantengeografisch Onderzoek van den indischen Archipel en Wegener's Verschuivingstheorie. Tijdschr. Nederl. Aardrijksk. Genootsch., 47:553–581; maps 6–7.

ignore the biology of Malaysia from which, as a center of origin and dispersal, it seems certain that a large number of the present Polynesian types of plants and animals have been derived.

Within Malaysia, in large measure because of its geological history, there developed two great centers of origin and dispersal; one was the Borneo-Java-Sumatra-Malay Peninsular part of ancient Sundaland, the other the New Guinea part of ancient Papualand. Plants and animals extended their ranges from these two centers: from the first, most of them went north into the Asiatic continent and northeast into the Philippines; and from the second, they went north through Gilolo, the Moluccas, and Celebes into the Philippines, south into eastern Australia, and east into Polynesia.

Plant Communities of the World

By Eduard Rübel

COMMUNITY is the sociologic unity of any rank from the lowest to the highest. In a short synopsis only the widest ranks can be discerned, but one must tell how one builds them up and understands them. As fundamental unit one has the "association." Its definition, proposed by Flahault and Schröter and adopted by the International Botanical Congress of 1910, held in Brussels, runs, "An association is a community of certain floristic composition, of uniform habitat conditions, and of uniform physiognomy." This definition has proved very satisfactory, and is better than all the others which since have sprung up here and there. By composition is meant not only the list of species; it includes their abundance, dominance, sociability, constancy, fidelity, vitality, periodicity, rhythm. The constants and characteristics are the main feature; they form the normal characteristic combination of species. Something so very ecologic as an association can only have its conditioning cause from an environment of a certain ecologic uniformity. Physiognomy is the effect of habitat. Habitat is the ecology of environment; physiognomy is the ecology of the vegetation itself, which expresses itself by its morphology, including its anatomy (life form of the dominants).

Species combine to genera, these to families (characterized by the ending -aceae), these to orders, ending in -ales (femininum plurale), to classes, and to other subdivisions. Quite analogous associations, ending in -etum, combine to a "federation," as Du-Rietz proposed to the International Congress, or "alliance," as Braun-Blanquet calls it, with the ending -ion (originally proposed by C. E. Moss in 1910). The following unity is the association "order" ("subformation," DuRietz) with the ending -etalia (neutrum plurale) introduced by Koch. The recognition of the community orders of the world is not yet far advanced; very much remains to be done. Gapless further unions are not yet possible. With the highest unities of communities the situation is different; they come from another line of research—from the attempt at classification. This is an old task. Here, as everywhere in every science, works the fundamental need of the human mind for order, for grouping, so to be able to apprehend the infinity of things existing side by side. Only in orderly fashion can mind render account of things. An investigator needs a synthesis of his field of research, a system. We have systems in philosophy, we have systems of the plants of the world; we need a system of the plant communities of the world.

A plant community is something eminently ecologic; to ecology, then, must be paid the first attention in arranging a system. A very essential point is connected with the law of minimum and the replaceability of factors. The law of minimum, founded by Liebig for cultures, is also valid for natural plant communities—and for one's own self-discernment. Any factor can only be effective when other factors also act sufficiently. It decides the factor which is present in a minimum. A soil may be highly nutrient, yet the nutrient substances do not work if moisture is lacking. Water and sun accomplish nothing if there is no nutriment. The minimum factor becomes the deciding one. Which it is, varies. Therefore, a classification may not be founded on a single factor, nor on a few factors. The single factor, moreover, acts differently according to other factors accompanying it. Absolute numbers in a factor say very little; all is relative. Fifty centimeters of rainfall acts hygromorph in oceanic Ireland, xeromorph in continental Algiers. Temperature modifies the moisture factor. Factors not only modify others; they may replace them. Replaceability of factors is very important. It makes it possible for a vegetation to thrive in localities where various factors have changed, and this allows the spreading of plant communities. For the investigator, it makes the characterizing of vegetation difficult. Language employs factors for characterizing. A locality is judged differently, according as we emphasize the changed or the unchanged factor. Formerly, vegetation was grouped climatically and the change of situation by edaphic factors was neglected. Edaphically conditioned vegetation did not fit. These difficulties are solved if the replaceability of factors is duly taken into consideration.

The replaceabilities modify thoroughly the law of minimum. A replacing factor may raise the minimum of another factor or may lower it—Roosevelt has annihilated the hampering factor of lameness by an extraordinary factor of will. A species or a community may be well adapted to a climate and thrive if unlimited soil is at its disposition. But it may lack strength to battle against the competition of invaders. Good, thriving, natural vegetation in New Zealand has been dispossessed by invaders accidently brought into the country by man—invaders which had a stronger power of competition and therefore raised higher than the existing conditions the needed minimum for maintenance of the old vegetation. Dispossession was the result. Taking replaceability into account, edaphic factors find their modifying value in climatic bases for classifying vegetation. The entire ecology may be more or less grasped, and the system becomes more and more natural.*

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* More explicitly than can be done here, but still concisely, all these questions of general sociology are treated in my *Soziologie* ("Geographie der Pflanzen," *Handwörterbuch der Naturwissenschaften,* Bd. IV, p. 1044; Gustav Fischer, Jena.)

After trying all the systems published, I have come to prefer the following one, which is an emanation, a continuation of the system of Brockmann-Jerosch and Rübel, of 1912. The entire vegetation of the world can be included ecologically in comprehensive formation-classes, as follows:

The formation-classes of the world

1. Pluviisilvae	Rain forests
2. Pluviifruticeta	Rain scrub
3. Laurisilvae	Laurel-leaved forests
4. Laurifruticeta	Laurel-leaved scrub
5. Durisilvae	Sclerophyllous forests
6. Durifruticeta	Sclerophyllous scrub
7. Ericifruticeta	Ericaceous scrub (heaths)
8. Aestisilvae	Summergreen forests
9. Aestifruticeta	Summergreen scrub
10. Hiemisilvae	Raingreen forests (monsoon forests)
11. Hiemifruticeta	Raingreen scrub
12. Aciculisilvae	Needle-leaved forests
13. Aciculifruticeta	Needle-leaved scrub
14. Duriherbosa	Hardgrass prairie
15. Sempervirentiherbosa	Evergreen grassland (meadows)
16. Altherbosa	Tall herbage
17. Emersiherbosa	Emersed swamp vegetation
18. Submersiherbosa	Submersed swamp vegetation
19. Sphagniherbosa	Moss moor (Hochmoor)
20. Siccideserta	Dry deserts
21. Frigorideserta	Cold deserts
22. Litorideserta	Strand steppes
23. Mobilideserta	Wander deserts
24. Rupideserta	Rock deserts
25. Saxideserta	Stone (and wood) deserts
26. Aquerrantia	Phytoplankton (water floaters)
27. Solerrantia	Phytedaphon (soil floaters)
28. Aërerrantia	Phytaëron (air floaters)

The system here given accords with physiognomic-ecologic considerations. The innate ecology is seized in order to give expression to sociologic gradation, to prograding stages of organization. In this the system of communities is quite analogous to the systems of plants, which also are built up in progressive stages of organization. At the bottom of the list we put the floating communities, of very loose union. The least stable are those floating in the air, then those floating in the water, then those suspended in the ice. Also, small primitive organisms in and on the soil may be called floating. Above stands the stone and wood vegetation, still mostly one-layered without root competition; above these, in turn, the rocky grounds and other deserts with some open vegetation—open, it may be, on account of the rocky ground, the mobility of the ground (dunes, screes, alluvials), the cold climate (open tundra), the dry climate. Higher stand the closed communities: first, the swampy ones —submersed aquatic, emersed aquatic, moors; then the few-layered communities on land—tall herbage, meadows, prairies, short-grass communities. The highest organized types are the several-layered woody communities of shrubs, and especially of trees, forming the complicated forest communities, differing according to the climates.

For the purpose of a synopsis, it will be well to follow up these larger formation-classes, their ecology, morphology, and distribution. Of associations and other smaller unities, only examples can be given.*

1. Pluviisilvae: Rain forests.—Pluviisilvae are forests rich in epiphytes whose dominant plants consist of evergreen and often

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* A more detailed account of them will be found in my *Pflanzengesellschaften der Erde* (Verlag Hans Huber, Bern; 1930), where also a multicolored world map shows the distribution of climatic formation-classes. Brockmann-Jerosch, who did the map, has published a large wall map of the formation-classes (Justus Perthes, Gotha).

stem-flowering (cauliflоral) trees, usually without bud protection and with glabrous and glossy foliage. The climate this forest needs is hot oceanic, as found in the tropics. The tropical countries have an annual precipitation of from two hundred to four hundred centimeters, distributed rather evenly the year round. The mean annual temperature is high and uniform, the difference between the warmest and the coldest months being only from one to six degrees Centigrade. The vegetation looks luxuriant. As many as four or five stories are developed. It is the phanerophyte climate of Raunkiaer, in which high-grown species are plentiful. Warming (1892) counted four hundred species of trees within three miles' distance in Lagoa Santa, Brazil. Light is a minimum factor within the forest. The leaves are evergreen, though the single leaf lives not much longer than one year; but the defoliation is irregular the year round, so that the forest never stands bare. Rain forest is distributed in the tropics of Australia, Ceylon, the Sunda Islands, Annam, New Guinea, Central America, northern Brazil, and Africa.

The sociologic unities have been studied so far only in very few localities. From British Guiana we have a good detailed study by Davis and Richards. They distinguish five consociations. While in general in tropical forests the normal condition is that no one single species reaches plain dominance, four of these types have a dominant and only one follows clearly the plan of mixture. The Mora forest dominated by the strongly buttressed *Mora excelsa* occupies the lowest ground. It forms a broad strip along both banks of the Moraballi Creek and along the branch creeks. On the lower slopes of the smaller flat-topped hills lives the Morabukea forest type dominated by *Mora gonggrijpii*. This is much the darkest type of forest. The lower hilly land is covered by the mixed-forest association. Many species together form dominance; the most prominent are *Pentaclethra macroloba, Licania venosa, Licania laxiflora, Licania heteromorpha perplexans, Eschweilera sagotiana,* and *Ocotea rodioei,* followed by about eighty-five less plentiful canopy-tree species. The majority of these are the same as in the Morabukea and Greenheart types. *Ocotea rodioei,* the Greenheart, dominates the next type, growing on reddish brown sand "reefs." The most distinctive type, structurally and floristically more sharply distinguished from the other types than they are from one another, is the Wallaba association dominated by *Eperma falcata,* growing on the white sand of the high hill-ridges. The number of trees to the unit of area is very large; big trees are scarce; buttressing is almost absent. From the Blue Mountains of Jamaica, Shreve gives an account of montane rain-forest with three dominant species—*Clethra occidentalis, Vaccinium meridionale, Podocarpus urbanii*—which make up half the tree canopy.

2. *Pluviifruticeta: Rain scrub.*—Pluviifruticeta are scrubs rich in epiphytes whose dominant plants consist of evergreen shrubs, usually without bud protection and with glabrous and glossy foliage. Climatically there is no reason why scrub instead of forest should prevail. Edaphic and biotic checking cause scrub under the same tropic climate. Rain scrub is very limited. In the flood region of tropic shores lives the characteristic Mangrove of shrubs and small trees. Karsten writes about them: Root sprouts break forth from the stem and from the lower branches and reach, in an elegant bend, the soil; the stem of the Rhizophores dies away and the "tree" stands only on its stilt roots—a very curious sight. So in spite of a short trunk these "trees" are positively of shrub rank. At high tide only the crowns are visible, at low tide one sees them standing on a dense tangle of

root stems. Only few species can endure the strenuous habitat condition. Two associations are well known. The American Mangrove consists only of *Rhizophora mangle, Laguncularia racemosa, Avicennia tomentosa,* and *A. nitida.* The association grows on the tropic mud beaches and covers the shores as far north as southern Florida. The eastern Mangrove, Rhizophoretum mucronatae, is much richer in species. It has its center in the Malay Archipelago. Impoverished association specimens are found as far distant as southern Japan and New Zealand.

3. Laurisilvae: Laurel-leaved forests.—In Laurisilvae the dominant trees, if dicotyledons, have evergreen leaves which are usually glabrous, bright green, and at right angles to the incident light, relatively large intercellular air spaces often being present and the buds protected; if gymnosperms dominate, these bear broad evergreen leaves or scale-formed ones covering the twigs tile-fashion. These forests continue from the rain forests poleward and upward where the rain forests can no longer thrive on account of diminishing average temperature and increasing temperature variations, but like them they are correlated with regular rainfall, relatively high humidity, and uniform temperature—in all, a temperate oceanic climate. These forests are distributed in Pacific North America, Florida, Chile, Patagonia, the Canary Islands (beautiful laurel forest), Madeira, Portugal, Cape Province (Knysna), the Himalayas, Japan, New Zealand. The misty forests of middle and northern Florida and Chilean Valdivia are of this kind. They are mostly dominated by evergreen beeches, as, for example, *Nothofagus betuloides.* The climate has a mean temperature of only five to nine degrees Centigrade, but only nine degrees difference between winter and summer, with a great deal of precipitation all the year round.

A number of conifer forests place themselves in the Laurisilvae on account of their physiognomy and distribution, and apparently their ecology, which unfortunately is little known. The inner constitution of this systematic group does not allow a real broad leaf, such as that of the dicotyledons, but they do what they can in differentiating from the needle type. Scale-like spreading and tile-like covering of the mass of closely knitted leaves make something similar to a large broad leaf, glabrous with a certain dim gloss, and at right angles to the incident light. *Thuja gigantea* and *Tsuga heterophylla* have such forms. The same result is reached by the broadening of needles and the placing of one near another like a mosaic to make up big leaves, as in *Sequoia sempervirens.* An ecologic anatomical research concerning these forests is highly desirable; here they have only been placed by analogy; because in distribution and habitat they are similar to the well-known dicotyl laurel woods, it is assumed that they need a similar climate. Such predictions have proved right in the past (e.g., concerning heaths); may future studies prove this one right also. Examples of these forests are found in the northwestern United States, in the Coast Range and the western Cascades with their mild winter (Seattle, mean January temperature, +4.3°), cool summer (mean, July, 17.7°), small difference (13.4°), great quantity of fog (only 25 to 40 per cent of the possible sunshine), and grizzly "Scotch" rain. A dense canopy of giants with elegantly hanging branches makes a wonderful impression. The hemlock, *Tsuga heterophylla,* with a mosaic of parted needles and a sideways swing of branches, gathers all possible light in the dim, dusky wood. Still broader in foliage is the scale-leaved *Thuja gigantea.* In the Cascades, fire has not rarely destroyed these associations and a Douglas fir forest has sprung up as fire succession. The laurel leaf also occurs in the undergrowth. Of evergreens I noted, for example, *Gaultheria shallon, Linnaea americana, Berberis nervosa, Viola sempervirens, Chimaphila umbellata, Vaccinium parvifolium,* and *Pyrola bracteata.* I should like to know whether the western coast of Canada and Alaska have such forests, with ecology and sociology to rank them among Laurisilvae. An ardent desire for studies! Near San Francisco is the Sequoietum sempervirentis in the coastal mountains where cold sea-winds produce a fog belt for the greater part of summer. The redwood spreads glossy needle twigs, causing reflexes like regular laurel leaves; more so does *Arbutus menziesii.* There occurs also an azalea, *Rhododendron occidentale,* the laurel-leaved shrub *Berberis nervosa,* and the low wintergreen, *Gaultheria shallon.* South America's Araucaria forests belong also to this class of formation.

4. *Laurifruticeta: Laurel-leaved scrub.*—This is the same as Laurisilvae, but scrub instead of forest. In the oceanic southern hemisphere this glossy-foliaged scrub occurs upward to the wood limit, forming, as in South America, a scrub belt above the forest. The same is done in the Caucasus by the association of *Rhododendron caucasicum.* On the whole, such scrubs are not so independent in the northern hemisphere, but for the most part are biotically influenced, or, in a cooler climate, they take refuge as underwood in forests whose dominants belong to a climatically cooler type, yet create under their canopy a locally more favorable climate. This telescoping of types presents a complication. To be cited are the true laurel scrub Lauretum nobilis in the Mediterranean, the Prunetum laurocerasi, and Rhododendretum pontici in the Caucasus.

5. *Durisilvae: Sclerophyllous forests.*—The dominants in Durisilvae are trees with sclerophyllous foliage or green axes functioning as leaves. Sclerophyllous leaves are evergreen, mechanically

stiffened, and leathery, usually reduced in size, often hair-clad. They avoid hot sun radiation by standing obliquely to the light or presenting only their edges directly, as in Eucalyptus. Durisilvae thrive in the typical Mediterranean climate. A moist, mild, oceanic winter is there combined with a dry, hot, continental summer, and spring and fall rains occur, and winter rains in the southern parts. On the whole it is not a good tree climate; scrub has a greater importance in it than in other climates. Durisilvae occur in California, in the Mediterranean, in Australia. Around the Mediterranean are the forests of stone oak, *Quercus ilex,* and cork oak, *Quercus suber,* the olive groves, the date palm, the Casuarina forest; in Australia, the Jarra forest with dominating *Eucalyptus marginata,* the Karri with *Eucalyptus diversicolor,* the Wandoo with *Eucalyptus redunca,* and others.

In California, Cooper worked out four associations of relative constancy and wide distribution. The moistest areas of Durisilvae are occupied by the tan-bark oak forest, the *Pasania densiflora—Quercus chrysolepis—Arbutus menziesii* association, and Pasanietum densiflorae, characteristic of the lower altitudes of the northern Coast Ranges. The *Quercus agrifolia—Arbutus* association is characteristic of the outer central Coast Ranges from Mendocino to Los Angeles County, and is particularly well developed in the San Francisco Bay region and southward to the Santa Monica Mountains. The *Quercus agrifolia—lobata* association occurs in the broad valleys and gentle foothill slopes of the central Coast Ranges. Higher altitudes are occupied by the *Quercus chrysolepis—kelloggii* association, which belongs to the higher Coast Ranges and southern California mountains and to the middle altitudes of the Sierra. I was shown a beautiful association of light sclerophyllous forest with grassy undergrowth when MacDougal took me up into the Santa Catalina

Mountains. The forest, 1450 meters above sea level, was dominated by three evergreen oaks—*Quercus emoryi, Quercus arizonica,* and *Quercus oblongifolia.*

6. *Durifruticeta: Sclerophyllous scrub.* — Durifruticeta are scrubs with sclerophyllous foliage or green axes, switch plants. In Australia this scrub is for the most part climatically conditioned, but in the other continents biotic and edaphic factors have originated and enlarged the scrub areas enormously. From Australia is known the eucalyptal Mallee-scrub, the acacial Mulga-scrub, the Brigalow-scrub, and others; from Cape Province, the Fynbosch. The Mediterranean Macchia and Garigue is to be divided into a series of federations and associations so far not entirely unraveled. The most luxuriant is the Arbution, in which are the Arbutetum, dominated by the glossy *Arbutus unedo,* the Ericetum arboreae, and the Fruticiquercetum ilicis, dominated by the shrubby-formed *Quercus ilex.* In the cist rose federation may be counted the Cistetum monspeliensis, the Cistetum ladaniferi, and the Cistetum salvifolii. The Garigue of Spain includes different types of the Tomillares; the Dwarf-palm scrub, Chamaeropetum humilis, is also a good association; in Greece the Phrygana types, in southern France large areas of Quercetum cocciferae, the Kermes oak, dominating.

In California the "climax chaparral association" (Cooper) is the dominant community over the whole of the southern Coast Ranges and the mountains of southern California and northern Lower California. *Adenostoma fasciculatum* is for the most part the dominant species, but many evergreens are conspicuous and quite a few consociations will be recognized within the association. Many species of Arctostaphylos and of Ceanothus are prominent. With its center in the northern Sierra, the mostly biotically conditioned (fire) "Conifer forest chaparral association" covers the middle altitudes. Species of Quercus and Arctostaphylos and others are preponderating.

7. *Ericifruticeta: Ericaceous scrub (heaths).*—Ericifruticeta are scrub communities whose dominants bear ericoid leaves. The ericoid, rolled-up structure gives a tubular form which makes the leaves stiff without the necessity of special mechanical tissue. The heaths live in a cool, moist, oceanic climate. They are extremely well developed in Norway, and they follow the coast regions of Great Britain, Germany, and France to the Canary Islands, through cool, oceanic, subalpine belts of mountains. They look xeromorph, but Stocker has proved that they are mesophytes to hygrophytes. These studies have proved that we were right in placing these communities here by their habitat, at a time when the ecology was yet far too little known. The smallness and ericoid form of the leaves stiffens them against being torn and wilted by the very heavy winds of these countries. The xeromorph appearance is an unintended by-effect. The soil is leached and poor in salts; and heavily transpiring evergreen heath scrub gets out the best of it, as the vegetative season is prolonged by the oceanic climate with mild winters. Calluna heath was the association which awakened the first phytosociological ideas in Alexander von Humboldt. It occurs on wide stretches in Great Britain, the Netherlands, northwestern Germany, and southwestern Sweden. A moister association is the Ericetum tetralicis; a special Cornwall heath is the Ericetum vagantis. Other heath communities are found in Portugal, in the upper part of the fog belt of the Canary Islands, and elsewhere. A well-developed heath system are the arctic and the alpine dwarf shrub communities. Remarkable for richness in species (about four hundred species of Erica) are the heaths of Cape Province.

8. *Aestisilvae: Summergreen forests (deciduous forests).*—The dominant trees become leafless regularly in the cold season; their buds are always protected. A warm moist summer allows them a very high water balance. Aestisilvae are the widely extended forests of middle Europe, eastern Asia, and eastern America. The beech woods of Europe are being closely studied at present in many countries. The preëminent forest of the eastern United States and southeastern Canada is the beech-maple forest; toward the drier Middle West it changes through a transition of maple-elm forest into extensive oak forests. Deciduous oak forests occupy the stretches of moderately continental climate and struggle for area with the more continental prairie. The ratio of precipitation to evaporation is 80 to 100 per cent, and in beech forests it is more than 100 per cent.

In southern Switzerland, below the beech belt on calcareous soil are oak forests (*Quercus sessiliflora*); on siliceous soil, chestnut forests (*Castanea vesca*). Wet or moist forests in running water are the "Auenwälder" of Europe, forests of *Alnus incana* with willows, many lianas such as hops (*Humulus lupulus*) and *Clematis vitalba*. The equalizing action of water permits the Populus communities to follow the rivers far into the African desert, and *Populus fremonti* and *Fraxinus tomei* in the river bed at Tucson into the Arizona desert. In stagnant water, *Alnus glutinosa* dominates the English "Carr" and the "Bruchwald" of the European continent. Near these may be ranged the *Taxodium distichum* community of the Great Dismal Swamp in Virginia and North Carolina.

9. *Aestifruticeta: Summergreen scrub.*—Summer scrub is biotically and edaphically conditioned; a few of its constituents semiclimatically. Where the climate permits closed deciduous-leaved summer vegetation, this suffices, as a rule, for tree

growth. Well known is the federation Quercion pubescentis, or "Shiblyac," a sub-Mediterranean, submontane scrub widely distributed in Bulgaria, Rumania, and Jugoslavia, and in Italy westward to the Spanish Monte Bajo and eastward to the Caucasian countries. Dominants are *Quercus pubescens, Berberis vulgaris, Viburnum lantana, Syringa vulgaris, Cotinus coggygria,* and *Paliurus australis,* among others. Similar scrub of oak, Rhus, Fendlera, and Cercocarpus, I have passed in the Wasatch Mountains, as well as near Palmer Lake on the mesa.

In the Alps, moist siliceous slopes where avalanches discourage the growth of breakable wood are clad with green-alder scrub (*Alnus viridis*), a thicket of very flexible twigs.

10. Hiemisilvae: Raingreen forests (monsoon forests).—The dominant trees of these forests shed their foliage in dry hot summers, but burst into leaves with the beginning of a rainy season. Leaves are mostly small and compound in accordance with the continental tropic climate unfavorable for tree growth. Green bark often assists in assimilation. In Africa these raingreen forests—thorn forest, savannah forest, or monsoon forest—cover very large areas from Portuguese West Africa through northern Rhodesia to the Congo, Tanganyika, and North Bechuanaland, as well as on the south side of the Sahara. Many species of Acacia are dominants. They are also frequent in Asia and in South America, as, for example, the catinga and monsoon forest on the dry calcareous hills of Minas Geraes. A Prosopetum juliflorae is conspicuous on the permeable sand and clay soil of the southern shore plains of Jamaica.

11. Hiemifruticeta: Raingreen scrub.—Inward on the continents, trees give way to bushes. This scrub fringes the deserts and enters them at edaphically moister points. The association of the screw bean and mesquite (Prosopetum pubescentis) cover in the Salton Sink in southern California areas is influenced by the level of underground water. For the greater part of the year this scrub stands leafless, but when rain falls the bushes produce very quickly their small compound acacious leaves. Between these bushes I noted *Atriplex canescens* and *Atriplex lentiformis* and, conspicuous in the undergrowth, saltgrass, *Distichlis spicata.* Important for the association are also *Acacia greggii, Acacia constricta, Flourensia cernua,* and *Larrea mexicana.*

12. Aciculisilvae: Needle-leaved forests.—The dominant trees bear needles. The needle leaf is small, linear, mostly with special mechanical strengthening, and, with few exceptions (Larix), evergreen. Many conifer forests belong in this association, but I have also found conifers in the Laurisilvae and Taxodium in the summer forests. The climate is cold and continental, the vegetative season short. The forests grow in the subalpine belt and the subarctic zone, in the inner parts of continents and in inner alpine valleys, edaphically, where the soil is too poor for broad-leaved forests—on sand, on flat ground, in swampy ground poor in oxygen. Large parts of the northern hemisphere between forty-five to fifty and between sixty-five to seventy degrees of latitude bear such forests. The Piceion excelsae covers enormous stretches in Europe and Asia. The unpretending *Pinus silvestris* can form communities almost anywhere, but has hardly the strength to compete with other trees for which the habitat is good enough. The highest tree-bearing areas in the Alps belong to larch and arolla pine forests (*Larix europaea, Pinus cembra*).

In the northwestern United States is a subalpine Aciculisilva of *Abies lasiocarpa* and *Tsuga pattoniana.* In more continental and more southern Colorado the formations lie higher and separated, a subalpine Pinetum aristatae from 3600 to 3400 meters altitude and the Piceetum engelmanni from 3400 to 2700 meters. In the same belt in California, dominants are *Pinus jeffreyi* and *Abies magnifica* from 2500 to 2200 meters altitude. To the lower part of that belt probably belongs also the Washington forest, between 1400 and 600 meters altitude, of *Pinus monticola* and various species of Abies. In the more arid area *Pinus ponderosa* forms forests around 1000 meters altitude in Washington and from 1900 to 2700 meters in Colorado. Moister areas of the same belt are governed in California from 1500 to 2200 meters altitude by *Abies concolor* (in these forests are the "Big Tree" groves). This forest prevails in Arizona around 2400 meters altitude. In the same belt live enormous Pseudotsuga forests, but the Douglas fir spreads so widely by reason of biotic factors that its forests derive from diverse causes. The lowest parts of oceanic Washington have been mentioned in the discussion on Laurisilvae.

A remarkable phenomenon occurs at the tree limit in the Cascades. While the ascending crests are clad with trees, perpetual snow lies on open flat places. In these mountains the climatic snow limit lies at 2000 meters altitude, the tree limit at 2300 meters. This brings about the very interesting situation that these important lines not only are near each other, but actually transgrade. In the Swiss Alps the forest limit remains at 700 to 1000 meters below the perpetual snow limit; but in the very oceanic climate of Washington State, forests can thrive above the climatic snow-line, and its alpine vegetation, which only begins above the forest limit, thrives even higher. Phanerogams are known there up to 3200 meters altitude, that is, 1200 meters above the snow limit. A part of the subalpine belt and the whole of the alpine belt fall here into the niveal belt. We feel carried back to the glacial period. What interesting problems wait here for study! If the Alps in the glacial age had a climate similar to that of western Washington today (the glacial age snow limit of the Wallis coincides with Washington's of today), the greater part of the Alpine flora may have survived. The country north of Washington and into Alaska would surely give still better parallels. A study of this vegetation in respect to these questions of ecologic dependencies is ardently desired, nay, even demanded!

13. Aciculifruticeta: Needle-leaved scrub.—These unpretending communities occur where more pretentious ones give way: in the mountains near the tree limit, and lower down when edaphically the conditions are less favorable, as on desolate calcareous slopes and badly aërated raw humus soils. The best known is the dwarf-pine scrub (*Pinus mugo*), which covers much area in the Alps, partly edaphically, in larger part biotically enlarged by forest-felling in former times.

14. Duriherbosa: Hardgrass prairie.—Duriherbosa are grasslands in which the dominant species have vegetative organs more strengthened by the development of the mechanical tissue than by turgescence, and which die down in winter. The climate is fairly continental with dry periods (semiarid to semihumid). Essential is the seasonal repetition of the precipitation; there are early summer rains just at the vegetative season, which encourage the growth of a grass sward. Two groups are to be distinguished—one winter-cold, the other warm (savannah); in common are the deciding dryness and the summer rains.

Hungarian and southern Russian sward steppes are conspicuous, called "pussta" in Hungary, "black earth steppes" in Russia. Dominant grasses are *Stipa capillata* and *St. pennata, Andropogon gryllus,* and, on the best black earth, *Festuca vallesiaca* and *Koeleria cristata.* Similar communities are found in locally dry continental areas in middle Europe, as in the Wallis of Switzerland; a fine Festucetum vallesiacae, and related unities, are found similarly in the Bohemian foothills and in the Jugoslavian Velebit Mountains. The most famous communities of this class are the prairies and great plains of America, so well studied by Clements, Shantz, Livingston and Shreve, Weaver and Fitzpatrick, and others, that I need not go into details.

The decided continentality of the Duriherbosan climate must rely on the strong change of dry and wet without great temperature differences. The areas with rich savannah grasslands cover wide stretches in Brazil, the Argentine, Australia, and especially in Africa. With increasing coldness, the communities merge toward steppe prairie, and where the climate becomes less hostile to trees one finds gradual transitions to Hiemilignosa.

15. Sempervirentiherbosa: Evergreen grassland (meadows).— The turgor for the most part suffices to keep the dominant grasses and herbs in their shape, and mechanical stiffening is therefore slight. These meadows have no pronounced winter rest; they sprout whenever temperature permits. They prevail in a cool oceanic climate poleward beyond the tree limit, in the mountains above the tree limit, edaphically in flood areas of sea and rivers and on windy coasts. Most meadows, all middle European meadows of the plains, are biotically conditioned (half-culture) and would turn into forests if left alone. Many leaves die in winter, but younger ones in all stages are always present and new ones are formed. The plant is evergreen, but the single leaf is not. Whenever I dug in the Engadine in the cold months when the temperature of the air was far below zero, I found the local habitat under the heavy snow cover to be around zero and the vegetation green, always ready to assimilate if the temperature should rise above zero. Swiss sociology has always favored the study of meadows, from the time of Stebler and Schröter's classical studies. It has much to do with alpine as well as lowland agriculture.

Arrhenatheretalia, manured meadows, are about the same all over Europe, since similar practice has brought about a convergence everywhere of the same factors. Caricetalia curvulae and Salicetalia herbaceae, "Schneetälchen"-Gesellschaften, grouping around the twist sedge association (of *Carex curvula*) and the herb willow association (of *Salix herbacea*), are the highest alpine and best studied meadow communities. The latter are also well distributed in Scandinavia.

16. Altherbosa: Tall herbage.—Tall-growing herbs dominate in this. It is an exacting vegetation, greedy for humous, nutrient-rich soil, and it occurs where forest and scrub for one reason or another are absent. The Adenostylion or "Karflur" in the subalpine belt of the Alps is developed in an Adenostyletum alliariae, a Peucedanetum ostruthii, a Chaerophylletum villarsii. Mammoth tall herbage, as much as four meters high, occurs in the Caucasus under the lead of Heracleum mategazzianum. In the Arctic, *Angelica archangelica* dominates, man-high in well-sheltered dales in Greenland. The "lair herbage," Rumicion alpini, around the alpine dairy huts on the overmanured soil shows as dominant the big *Rumex alpinus* or *Senecio alpinus,* or, in the Caucasus, *Telekia speciosa.* A successional stage of tall herbage after wood-felling or forest fire is dominated by *Epilobium angustifolium,* called "willow herb" or "willow rose" in Europe, charming with its red spikelets in the little wood openings, but detestable as "fireweed" over wide American lands where lumber companies have devastated the country by their logging operations.

17. Emersiherbosa: Emersed swamp vegetation.—The dominants in this community are marsh plants which root in water-covered or saturated soil, but which have their leafy shoots above the water surface sufficiently stiff to hold themselves erect. Water is an equalizing element, watery habitats are similar even in very different general climates; water plants are therefore ubiquitous and their communities are similar in different countries. The order of Molinietalia coeruleae consists of communities which have their roots, but not yet the stems, in the water. They make what are called sour meadows; agriculture gains litter. In the Molinion federation the association of the pipe grass, *Molinia coerulea,* is the most important; in the Parvicaricion, one counts in Switzerland the Schoenetum nigricantis; Juncetum subnodulosi, Caricetum lasiocarpae, the important widespread Caricetum fuscae, the alpine Eriophoretum scheuchzeri, and the alpine Trichophoretum caespitosi and pumili. The Phragmitetalia are new-land builders, pond communities. Of the Magnicaricion elatae by far the commonest is the Caricetum elatae (others are the Caricetum inflatae and Caricetum vesicariae), beautifully described in 1863 by Kerner as the "Zsombek" of the Hungarian lowlands, and by Pound and Clements on the Missouri, and by Schröter in Switzerland. Still more widely distributed is the Phragmition, with the Scirpeto-Phragmitetum communis, well known in many countries, as, for example, East Norfolk in England, and the enormous areas in the Danube and Volga deltas. If the water contains NaCl, one finds on all seashores similar communities, the associations Atriplicetum portulacoidis, Juncetum maritimi, Glycerietum maritimae, and very commonly Salicornietum herbaceae and Spartinetum.

18. Submersiherbosa: Submersed swamp vegetation.—This consists of macrophytic aquatic plants with submerged or floating leafy shoots. The influence of climate is minimal. Differences in temperature are still of some influence, but rather on the floristic composition than on the ecology. Salt content divides groups; also the rooting in mud or fixation on stone. Therefore we have four large groups or orders—the mud-rooting sweet-water Potametalia or Limnaeas, the mud-rooting salt-water Enalids, the stone-fixed Limno-Nereids or Encyonematetalia, and the Halo-Nereids; and to be added to these are the swimmers Pleuston or Hydrocharitetalia.

Warm water knows as Limnaea the beautiful *Victoria regia* with its associates; colder water, the lake roses (water lilies) Nymphaea and Nuphar; in the alpine belt, *Sparganium angustifolium* and *Hippuris vulgaris* and *Ranunculus flaccidus;* in the north, *Stratiotes aloides;* in America, *Eriocaulon septangulare* or *Elodea canadensis;* in Lake Titicaca, Ceratophylls and Potamogetons; in deeper waters, Charas and Nitellas. Enalids are the shore-covering subaquatic sea-grass meadows of *Zostera marina* and *Z. nana;* in the Mediterranean, Posidonietum oceanicae. Chlorophyceae and Cyanophyceae cover the stones of lake shores, as Limno-Nereids. Halo-Nereids are plentiful. In northern Europe live the well-studied algal communities of Fucaceae, Laminariaceae, and others. I never forget the amusing California community of sparse *Pelagophycus gigantea* with their mysterious floating heads, and the subaquatic dwarf-palm forest of *Postelsia palmaeformis.*

Ecologically, we have to place here also the Pleuston, the floating sargasso meadows of the ocean, and the water lens, Lemnetum, of ponds.

19. Sphagniherbosa: Moss moor (Hochmoor).—These communities depend on aërial water rather than telluric; they form swamps and produce their substratum by their own vegetation, especially by a Sphagnum covering. The climate is cool oceanic. Moss moors have a wide distribution in Scandinavia, Great Britain, Ireland, and in northwestern Germany in Europe. Northern North America also has Hochmoor, and, in the southern hemisphere, so do the Antarctic islands, Patagonia, Tasmania, New Zealand. The habitat is peculiar. Osvald groups these communities in Europe into four large types or federations—probably: (1) the western "ground covering," *Eriophorum vaginatum* Hochmoor, in England, Scotland, and Ireland; (2) the flat moss moor, *Sphagnum rubellum* Hochmoor, in southwest Sweden, along the Norwegian west coast, in low altitudes of the northern Scandinavian mountains, and in northern Finland; (3) the truest moss moor, *Sphagnum medium* Hochmoor, in southern and central Sweden, southwestern Finland, the Baltic countries, northern and northwestern Germany, and the mountainous areas of middle Europe (cold windy valleys of the pre-Alps and cold moist Jura heights in Switzerland); (4) wood-moss moor, *Sphagnum fuscum* Hochmoor, with *Pinus silvestris, Ledum palustre, Sphagnum angustifolium,* in eastern Sweden, Poland, Finland, Russia—in all the less oceanic areas.

20. Siccideserta: Dry deserts.—These are open communities. Larger plants do not exert any marked influence on any lower story which may be present. They are conditioned by the dryness of the climate. They lie in the great subtropical high-pressure zone of the earth. Temperatures may be hot or cold; the low amount of precipitation and its irregularity are decisive. Great deserts are the Eurasian, North African, western American, Australian, and South African.

Artemisia steppes: The Caspian (Asia) Artemisia scrub desert includes an Artemisietum maritimae incanae and, in saltier dales, Artemisietum pauciflorae. Well known are the extensive sagebrush deserts in western North America—an Artemisietum tridentatae with a Kochietum vestitae on loam and an Atriplicetum confertifoliae on a lower, moister level. The corresponding communities in Algeria-Tunisia are the Artemisietum herbaealbae and the Stipetum tenacissimae halfa grass-scrub desert. The halfa grass is stiffened by cellulose; its leaves are pluriennial, and therefore ecologically it is a shrub.

Where conditions take on a more extreme character, there are deserts of dry squarrose shrubs with reduced foliage. Most shrubs are thorny and have small, gray-green, leathery, evergreen or only raingreen leaflets. These are the thornbush deserts of Algeria, Tunisia, Egypt, and a most unusual one in the alpine belt of Teneriffa, the Retama Blanca desert of *Spartocytisus supranubius.* In South Africa is the large Karoo desert. Still more exacting on the vegetation is dryness and salt content combined. We find salty dry deserts in southern Russia, in Tunisia, Algeria, and around Great Salt Lake in Utah.

Prominent in this class are the succulent deserts. In Africa, succulent Euphorbiaceae are building up communities; in America (that is, in Mexico, Texas, Arizona, and New Mexico), Cactaceae. In the Bajada, *Larrea tridentata* is dominant, accompanied by the oddest forms of Opuntias. On the slightly inclined deep-soil talus stands the Parkinsonietum microphyllae including the local miracles, *Cereus giganteus,* the fleshy telegraph pole, and the stem-assimilating thorny ocatilla, *Fouquiera splendens.*

21. Frigorideserta: Cold deserts.—The vegetation of these deserts consists mostly of herbaceous perennial, rarely woody, plants, usually of fresh green color, and frequently of tufted, rosette, cushion, or creeping habit. They are climatically conditioned. Cold has the effect of dryness, since water for a great part of the year is in the form of ice and snow, unavailable for plant growth. Cold deserts are the most polar communities, horizontally the token of the high arctic zone, vertically of the niveal and subniveal belt. The alpine group has strong sun radiation in the short season; the arctic, less radiation but very long days; other factors are about the same.

In the High Alps such desert communities on fixed rubble are a wonderful symphony of colors. In the siliceous Androsacetum alpinae gleams the deep blue *Gentiana bavarica subacaulis,* changing with the delicate rose of *Androsace alpina* cushions and the sky-blue heavens' herald, *Eritrichium nanum.* Other communities are the Oxyrietum digynae, the Allosoretum crispi, and, on calcareous soil, Arabidetum coeruleae. The New Zealand niveal belt has the "vegetable sheep," *Haastia pulvinaris.* To the arctic cold deserts belong open tundra, the "fell field" of Warming, and the "rocky flat" of Ostenfeld.

22. *Litorideserta: Strand steppes.*—These are deserts developed under the influence of the neighboring sea where the atmosphere is full of salty spray. Rock-cliff strand steppe is the Senecionetum cinerariae, which is well developed on Mediterranean shores. As dominant, glitters the silk-hairy *Senecio cineraria.* Slightly darker is the also hairy, abundant, *Helichrysum angustifolium.* Corsica's Iles Sanguinaires have in this association their endemics, *Nananthea perpusilla* and *Evax rotundata.* Southern France has on its calcareous shore a similar association, the Artemisietum gallicae. The surge-sprayed lava rocks of the Canary Islands bear a most unusual type of this class, the Limonietum (Statice). A large number of purely endemic Limoniums spread their flower-veils in the most delicate gradations from lilac to blue to violet to red, and color for a short springtime the brown rocks. Flat shore-strand steppe is dominated in northern Europe by *Salicornia herbacea* with *Festuca thalassica,*or,on more sandy

soil, *Salicornia perennis* and *Atriplex portulacoides.* On the Mediterranean shores, *Salicornia fruticosa* is the main plant; in southwestern Australia, *Salicornia australis;* on Java, *Ipomoea pescaprae;* on the Moluccas, Canavalia; on Asiatic shores, *Spinifex squarrosus.*

23. *Mobilideserta: Wander deserts.*—The desert character of open vegetation is caused by the mechanical action of the unstable substratum. The mobility of the soil is a peculiar factor with formidable influence on the vegetation, demanding a particular ecology against its being torn away or buried. According as the mobility of soil is caused by wind, by gravity, by water, or by man, there are different groups: shifting dunes, steep screes, and shifting river alluvions. Ammophiletum arenariae is the main shifting-dune association all over Europe and America, with more or less slight variations. The English Lancaster coast has a foredune dominated by *Agropyron junceum;* Michigan, one dominated by *Calamovilfa longifolia.* Salt-water and sweet-water dunes are closely related.

The calcareous Alps have a fine sliding rubble vegetation around the Thlaspeetum rotundifolii, with *Trisetum distichophyllum, Papaver alpinum sendtneri* (white), and other plants, a fine scree on the Pilatus, for example. The eastern central Alps have an association with the pretty yellow *Papaver aurantiacum.* On the screes on Mount Garfield in the Rocky Mountains I saw, especially, Paronychia and *Silene acaulis.*

On alluvial ground in the Swiss Alps, *Myricaria germanica* is dominant from the plain up to 2000 meters altitude. In the higher localities on glacial river alluvium a subassociation is dominated by the red big-flowering *Epilobium fleischeri.*

Somewhat similar to the alluvium turned over about once a year by the high waters are the artificially turned-over soils, the arable ground. Treated every year in the same way, this ground has developed rather stable communities in two orders. The Segetalia, sown cultures, plowed once a year, have in middle Europe a weed community, Agrostemmatetum githagonis. Generally distributed is *Agrostemma githago;* brilliantly blue and red shine *Centaurea cyanus* and *Papaver rhoeas;* characteristic also are *Spergularia arvensis, Pisum arvense, Lunaria vulgaris.* Olitoria, hoed cultures, truck crops, are both plowed and worked over, in the season, by hoeing. These crops, such as potatoes and other vegetables, are not only manured and hoed, but often are watered also, and vegetation is somewhat hydrophilous. We can call the association Chenopodietum polyspermi, by reason of the frequent *Chenopodium polyspermum* accompanied by *Panicum crusgalli, Mercurialis annua, Euphorbia peplus, Amaranthus ascendens, A. retroflexus, Polygonum persicaria,* etc.

24. Rupideserta: Rock deserts.—This is the chomophyte vegetation of rocks which is dependent on detritus on the rock or in crevices, and thus is clearly influenced by the rock habitat. (When crevices become large, or detritus plentiful, this latter influence ceases and we have stony forests or grasslands.) In the detritus on the rock the habitat of the exochomophytes is rather xeric, and in the crevices with the chasmochomophytes, or chasmophytes, it is not. The prime condition is edaphic; climatic factors noticeable are altitude and exposure, both of strong influence on the local climate. Rock deserts are found locally almost everywhere in mountains, in erosion valleys, and on slopes and cliffs in the lowlands. In the Swiss Alps are to be distinguished the Potentillion caulescentis, on a calcareous habitat and with a montane-subalpine association characterized by *Potentilla caulescens, Kernera saxatilis, Asplenium rutamuraria, Lilium croceum,* and *Globularia cordifolia,* among others, and an alpine-niveal belt association dominated by the firm cushions of *Androsace helvetica,* accompanied by *Draba tomentosa* and others. The corresponding siliceous-rock vegetation gravitates in the subalpine belt around *Asplenium septentrionale* and several Sedum and Sempervivum species, and in the alpine around *Androsace multiflora, Phyteuma carestiae* (eastern), *Ph. humile* (western), and *Primula hirsuta.*

25. *Saxideserta: Stone (and wood) deserts.*—This is the Lithophyte vegetation of stones and wood, especially bark, growing directly on firm, not disintegrated substratum. Bark vegetation is similar to and often identical with the stone vegetation, especially with calciphobes (Gams). Mosses, and especially lichens, cover the rocks as well as bark in multicolored mosaic. The communities have been well studied in Fenno-Scandinavia by Sernander, DuRietz, Hayren; in the Swiss Alps by Eduard Frey, Ochsner, Gams. The other large group are the Algetalia, algal communities coloring more or less perpendicular rocks, especially Gloeocapsae and related species.

26. *Aquerrantia: Phytoplankton (water floaters).*—This community consists of microphytes free-floating in the water. Communities specialize with the content of salt, oxygen, humus. Also the snow contains its own kryoplankton according to its more solid consistency, and the floating of this growth is less mobile.

27. *Solerrantia: Phytedaphon (soil floaters).*—Microphytes, myxomyceae, schizomycetes, mucorineae, form communities in the soil. They neither root nor adhere. One may call it a floating on solid ground, just as the chemical engineer speaks of "solid solutions."

28. *Aërerrantia: Phytaëron (air floaters).*—Microörganisms float freely in the air; their connection is extremely loose, wind causes rapid changes, yet perhaps they occur in groupings.

Antarctic Plants in Polynesia

By Carl Skottsberg

"From the southeast, there is a slight but plausible indication of immigration."—W. A. Setchell, *Paths of dispersal,* in *Phytogeographical Notes on Tahiti, 1926.*

The recognition of an old Antarctic flora element, at least among the Phanerogams, dates back nearly one hundred years to the time when J. D. Hooker, on the famous cruise of the "Erebus" and "Terror" under James Ross, became aware of the biological resemblance between regions so remote from one another as Magellania, New Zealand, and the various islands on the threshold of the Antarctic Sea, and refused to believe that this could be satisfactorily explained merely by assuming an exchange across the wide expanses of water under the present physiographical conditions. Hooker had a presentiment that a natural explanation was hidden in the unknown history of the immense land mass known as Antarctica. Ross had discovered fossil wood of an extinct gymnospermous tree in Kerguelen, where at the present time no trees can grow, and it did not seem too audacious to postulate the former existence of an Antarctic land flora where there now is solid inland ice. By and by, proofs came that the Arctic regions had harbored a rich, warm-temperate or even subtropical vegetation. It became only a question of time when Antarctica would surrender its buried treasures. C. A. Larsen, the famous Norwegian whaling captain, collected the first fossil wood in western Antarctica in 1892, and ten years later the Swedish Antarctic Expedition, with Larsen in command of the vessel, discovered rich deposits from the Jurassic and Tertiary containing distinct connecting links between the floras of the lands on either side of the south polar continent. I was in the party, and I have taken an interest ever since in the history of the Antarctic flora and have tried to collect data bearing upon it. In 1915 I published an annotated list illustrating the intimate relations between subantarctic America and New Zealand.[12]* After I came to examine some of the Pacific floras (especially in Hawaii, where a small number of Antarctic genera occur, a strange sight in a Paleotropical insular world), I desired to take up the study of this element. The taxonomic basis is clear in respect to some groups, but in respect to others the position and affinities are not so well known and conclusions therefore are less safe. I have just had occasion to show how important monographic studies are, if we would arrive at something like definite results.[15] Time has not permitted me to make a complete study of the Antarctic flora, its history and migrations. I shall restrict myself here to occurrences of the representation of presumably Paleantarctic genera by geographically isolated species in the high Polynesian islands. These occurrences are few but very striking, and they offer a number of interesting and troublesome problems. Much more numerous are those Antarctic genera which, in the Pacific region, extend to New Zealand, southeastern Australia, New Guinea and, perhaps, Malaya without occurring in Polynesia. They do not seem to present exactly the same problems as do the genera which are the subject of the present study. Roads have been easier along the extreme western border.

Among the Antarctic-Pacific genera, more than one type of distribution may be distinguished. It is convenient to recognize one tricentric and one bicentric group. The former is represented in the Australasian, American, and African sectors; the latter is

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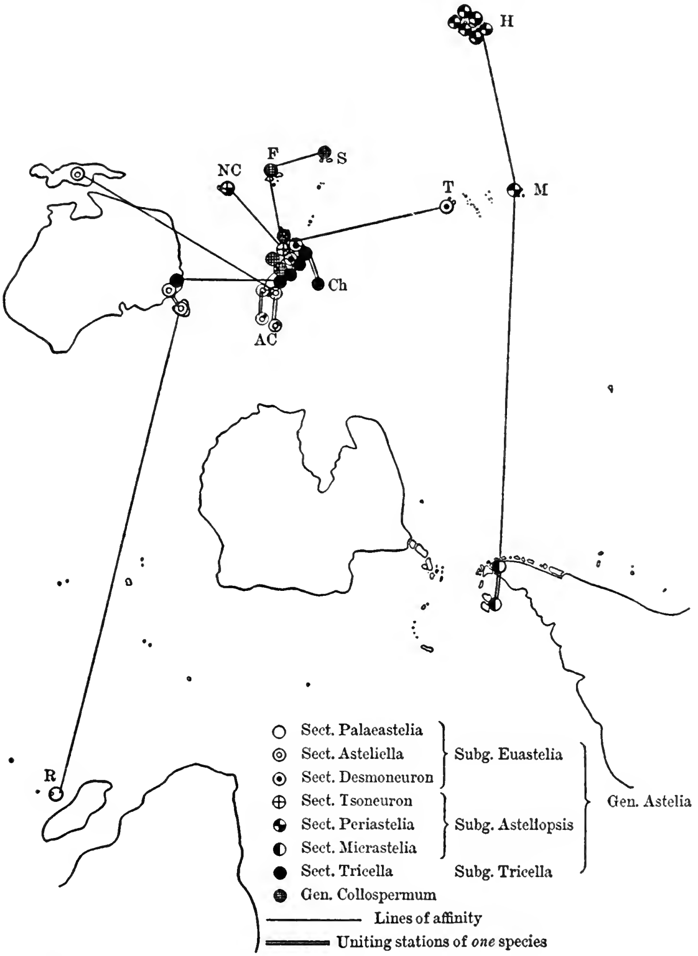
* Superior figures refer to items in the bibliography at the end of this essay.

absent from Africa (including Madagascar and the Mascarene Islands). If there were land connections between Antarctica and the surrounding continents, the African bridge certainly dates far back and its existence is altogether problematic; to those who do not believe in such connections, the remoteness of Africa from Antarctica and the scarcity of intervening islands explains why Antarctic types are so scarce in that sector. It is surprising that they exist at all.

We shall begin with a tricentric type, *Astelia,* a true Paleantarctic genus if there ever was one. In my sense,[15] it consists of 3 subgenera with 7 sections and 23 species. Its present headquarters are in New Zealand, where all subgenera and 4 of the sections occur, including 9 species. Two of the species extend to Auckland and Campbell Islands (or it may be more correct to say that the subantarctic species extend to New Zealand), and 1 to Warikauri (Chatham). There are species clearly related to the Neo-Zelandic ones in New Guinea (1), Tasmania (1), the Australian alps (2, 1 a variety of the Tasmanian sp.), New Caledonia (1), and the Society Islands (1). A separate section is formed by the 7 Polynesian species, 6 in Hawaii and 1 in the Marquesas, all closely related to one another. Finally, one species is endemic in subantarctic America, including the Falkland Islands, and one in the Island of Réunion off the east coast of Madagascar. Consequently, two of the three centers are represented by only one species each. But this does not make them less important. Each of the species forms a monotypical section. I have come to the conclusion that *Astelia hemichrysa* of Réunion represents the oldest existing type in this genus. The other members of the same subgenus are in the Auckland Islands, Campbell Island, New Zealand, Tasmania, Australia, New Guinea, and the Society Islands. A close study of distribution details and affinities, as shown in the sketch map accompanying this essay (p. 295), has given some interesting results. The position of sect. *Periastelia* (Hawaii and the Marquesas) is of special importance. From its geographical position, it seems natural to look for its closest relatives in the southwestern Pacific. But the Tahitian species belongs to a different subgenus. In New Caledonia and New Zealand we find members of the same subgenus, but they form another section not nearly related to *Periastelia*. We discover its nearest ally where we would not be likely to look for it, in the Magellanic *Micrastelia*. Simply because this occurs in America, we are not entitled to classify the Hawaiian species as belonging to an "American" element. *Micrastelia* is a stranger in the neotropical flora.

Collospermum, which I segregated from *Astelia,* perhaps should be mentioned here because it goes back to astelioid ancestors and is a Pacific genus of Antarctic affinity. It has 3 species in New Zealand, 1 in Fiji, and 1 in Samoa.

The distribution of *Gunnera* is significant. The Indomalayan-Australasian sector is the home of 2 of its 6 subgenera; *Pseudogunnera,* with a single Malayan species of wide range; and *Milligania,* with 8 species in New Zealand, 1 in Tasmania, and 1 in New Guinea. The African sector is inhabited by subgenus *Perpensum* with 4 species, 1 in South Africa, 1 on Kilimanjaro and Usambara, 1 in Abyssinia, and 1 in central Madagascar. (These may be regarded as subspecies of one species, but, even so, they have a long geologic history behind them.) The American sector is the richest. It has 3 subgenera: *Misandra,* with 3 species, ranging from the Falkland Islands and Tierra del Fuego to the tropical Andes; the monotypical *Ostenigunnera,*[10] recently discovered in Uruguay and probably less distant from the Neo-Zelandic *Milligania* than from any other subgenus; and *Pangue*



AC—Auckland and Campbell Islands
Ch—Chatham (Warikauri) Island
F —Fiji Islands
H —Hawaiian Islands
M —Marquesas Islands
NC—New Caledonia
R —Réunion
S —Samoa
T —Society Islands

Fig. 1. Distribution of Astelia and Collospermum.

("Panke" is a nonsensical corruption), with about a dozen species along the Andes, 2 in Costa Rica, 1 in Brazil, and 3 in Juan Fernandez, to which the 2 Hawaiian species are most closely related, whereas they have nothing whatever to do with the west Pacific *Pseudogunnera*. The Paleantarctic character of *Gunnera* is affirmed by the fairly close relation between *Misandra* and *Milligania*.

The distribution of *Acaena* is equally striking. G. Bitter, the monographer of the genus, recognized 10 sections. Numbers I (13 sp.), IV (1), and VI (1) are confined to the American sector; Number V has 6 species in subantarctic America, 1 in Masafuera, and 1 in Tasmania; VII has 26 species in South America, 1 in California, and 1 in Australia and Tasmania; VIII has 56 species in America (the Andes, Patagonia, Fuegia, 1 extending to South Georgia, Kerguelen, etc.), 2 in the African sector, 3 in New Zealand, and 1 polymorphic species in New Zealand and the surrounding islands, Tasmania, Australia, and New Guinea. Section II is endemic in the African sector (Cape, 1 sp.). Thus, this sector contains one endemic section, 1 endemic species of Section VIII in each of the islands of Tristan da Cunha and New Amsterdam, and endemic subspecies of a Magellanic species in Kerguelen, Crozet, and Prince Edward Island. The Australian-Neo-Zelandic sector has two endemic sections—IX with 1 species and X with 2 species. In addition, as we have already seen, V is represented by 1 species (Tasmania), VII by 1 species, and VIII by 4 species. Evidently the present center, with respect to both the number of species (97) and of sections (7), lies in extratropical South America. However, 5 sections are found in the Australian-Neo-Zelandic sector (9 sp.), and 2 in the African sector (4 sp.), and, if we believe that the stations in these two sectors are nothing but "branch offices" from the headquarters in South

America, we are probably mistaken. The endemic sections in Africa and New Zealand suggest relicts from a larger Paleantarctic area. These do not prevent us from recognizing, in the islands east of Magellania, signs of a more recent oversea migration in *A. adscendens,* although this species is represented by endemic varieties or subspecies in the various islands. The distribution of *Acaena* is a rather complicated matter.

After this somewhat lengthy introduction, we shall proceed to *Acaena* in Polynesia. It is represented by a single endemic species, which is found in the mountains of Hawaii, and belongs to Section III. This section contains only 2 species; the second is a native of subantarctic America and ranges north to the Andes of Valdivia. Again we are confronted with the mysterious connection between Hawaii and South America.

Another tricentric genus I shall quote is *Sophora* sect. *Edwardsia.* Some authors retain this as a separate genus because of its distribution and its winged pod, but the pod offers no reliable character; in the two Juan Fernandez species, which certainly cannot be separated from other Edwardsias, the pods are not winged. Even if we refuse—and I think we should—to let distribution determine the taxonomic position of *Edwardsia,* we recognize nevertheless the importance of distribution in reflecting the independent history of this section within the southern hemisphere. The American and New Zealand sectors are of about the same strength, with 3 species endemic in New Zealand, 1 in Chatham, 1 in Lord Howe Island, 2 restricted to southern Chile, and 2 to Juan Fernandez. One of the Chilean species, *S. macrocarpa,* occupies a rather independent position, whereas all the others are near relatives of the Neo-Zelandic species. The African sector contains 1 species in Diego Alvarez, allied to the Neo-Zelandic species, and 1 in Réunion. There are 2 species in

India. Of the Pacific species, the one in Hawaii seems to occupy a fairly independent position. The species of Easter Island, Rapa, and the Austral Islands are connected with *Sophora* in New Zealand and Chile. Thus we have an unusually even distribution of *Edwardsia* in fairly high latitudes around the southern hemisphere. It may not be right to classify the genus *Sophora* (in its wide sense) or the genera next to it as originally Antarctic, but the circumpolar range, combined with a perfect development of local endemic species, makes it quite possible that Antarctica has been the distributing center even if it was only a secondary center of evolution in the genus or group of genera.

Lastly, *Vincentia*—quite as often and, I believe, just as correctly referred to *Cladium* as a subgenus or section—deserves to be mentioned. About a dozen species are known, all except one, which occurs in the Philippine Islands, and perhaps another in Borneo, occurring south of the equator only. There are 1 (or 2?) in Réunion, 3 in the Indomalayan region (Philippines, Amboina, Borneo), 1 in New Zealand, 2 in Tahiti (1 of which is also in Hawaii), 2 in Samoa, 1 in Hawaii (same as a Tahitian sp.), 1 in Masatierra (Juan Fernandez), and 2 or 3 in Brazil. *Vincentia* is a natural group and some of the species are close together; it is interesting that *C. scirpoideum* of Juan Fernandez is closer to *C. angustifolium* of Hawaii and Tahiti than to any other species.

It may not be possible to call *Cladium* an old Antarctic genus, but, with respect to *Vincentia,* it is only natural to assume that Antarctica may have been the scene of part of its history. Even if we include *Eucladium* and *Baumea,* the original southern home of the whole assemblage appears to be fairly well established.

I feel justified in including *Weinmannia* among Antarctic genera. At present it approaches the Antarctic region with only 2 species—*W. racemosa* in New Zealand (also in montane forest on Stewart Island), and *W. trichosperma* in West Patagonia, where S Lat. 49° 30′ marks the southern limit of the genus—but it is eminently tricentric. According to Engler (in Nat. Pflanzenfam., ed. 2, with a few additions of later date), there are about 90 species in America (some 84 in tropical South America, 6 in Central America and the West Indies, and *W. trichosperma*); 15 in Madagascar (including the Comoro and Mascarene Islands); 26 along the western border of the Pacific (2 in New Zealand, 3 in New Caledonia, 2 in New Hebrides, 6 in New Guinea, 5 in the Malay Archipelago, 8 in the Philippines); besides 11 Polynesian (excluding New Caledonia and New Hebrides), namely, 5 Fiji, 2 Samoa, 1 Rarotonga, 2 Tahiti, 1 Rapa, and 1 Marquesas, of which *W. affinis* is found in Fiji and Samoa. Two special features interest us here: *Weinmannia* does not reach either the Australian or the African continent, a fact of certain importance; and the Pacific species form, with very few exceptions, a special section not represented elsewhere. It would seem plausible to suggest an Antarctic origin of the family Cunoniaceae; the genera are grouped around Antarctica, and leaves of *Caldcluvia* have been reported from the Tertiary beds of Seymour Island (Dusén).

The bicentric genera are absent from the African sector. It is true that *Uncinia* and *Lagenophora* occur in Tristan da Cunha, but the species are Magellanic and thus we cannot regard Tristan as an independent station in this connection. The same applies to Kerguelen with its Neo-Zelandic *Uncinia*. Both genera are typically Paleantarctic. Of the two subgenera of *Uncinia,* one is monotypic and confined to Magellania. The other has 2 sections. One of them (7 sp.) is entirely American, with 2 species in southern Chile, 1 species ranging along the Andes with an outlying station in Masafuera, 1 in tropical America, 1 mainly subantarctic species going east to Tristan da Cunha, St. Paul, and

New Amsterdam and west to Masafuera, and 2 species endemic in Juan Fernandez. The second and larger section has 4 American and 12 Neo-Zelandic species, and 1 which is credited to both regions. All the American species are found in southern Chile, 2 reach Tierra del Fuego, and one of these goes north to Central America and has a remote station in Masafuera. Of the 12 Neo-Zelandic species, 7 seem to be restricted to New Zealand, 1 reaches Tasmania and the Philippine Islands, 1 extends to Tasmania and Australia, and 2 are more widespread (1 being common to Australia, Tasmania, New Zealand, and Macquarie Island, ranging west to New Amsterdam and Kerguelen; the other extending from Auckland and Campbell Island to Australia, Tasmania, Lord Howe Island, and New Guinea); and finally, *U. uncinata* of New Zealand and Warikauri is also found in Hawaii, if Dr. Kükenthal's identification, as expressed in the Pflanzenreich, is correct.

In the Pacific there is a small group of related species of *Carex,* three of which recently have been described by F. B. H. Brown,[1, 2] *C. tahitensis* from Tahiti, *C. Stokesii* from Rapa, *C. feani* from the Marquesas, *C. Rechingeri* from Samoa, and *C. sandwicensis.* To the same assemblage belong two species from New Zealand and the Magellanian *C. Darwinii,* which is also credited to Warikauri and the subantarctic islands. However, to our present knowledge, these species do not form a closed group; near them are placed a number of Boreal species from the Arctic, North America, Europe, and Asia. It is quite possible that Antarctica is not involved in the history of the Pacific species. Students in plant dispersal will remark that the utricles of *Uncinia,* with their hooked rhachilla, are well adapted to be transported in birds' plumage, and carriage by wandering marine birds may account for the great range of some species and the occurrence in Tristan da Cunha, Kerguelen, St. Paul, New Amsterdam, and Masafuera of Magellanian or Neo-Zelandic Unciniae. Perhaps the presence of *Uncinia* in Hawaii and the Philippines may be explained in the same way. But it is surprising that no representative of it has been found on the high mountains of Malaya or the peaks of Melanesia and Polynesia.

Lagenophora is distributed in much the same way as *Uncinia.* The 7 species in New Zealand, together with the 4 in Australia (of which *L. Billardieri* ranges north to New Guinea, Malaya, and the Philippines), form the greater part of the genus. The 3 subantarctic-American species and the 4 Pacific species (1 Fiji, 3 Hawaii) are connected, the former with the small *L. pumila,* etc., the latter with the more robust *L. Billardieri.* In this genus, as in *Uncinia,* we do not find a closer connection between Hawaii and South America than between Hawaii and Australasia.

Finally, we have *Oreobolus,* a remarkable genus possessing the most primitive flower structure found in the family, and adapted to live in bogs in a very wet and chilly climate. Of its 5 species, 3 are endemic in New Zealand and eventually reach the subantarctic islands (1 of these also extends to Tasmania and the Australian alps); 1 is found in the Andes, Tierra del Fuego, and the Falkland Islands, with an outlying station in Masafuera; and 1 is endemic in the Hawaiian Islands. All are closely related. The Hawaiian species seems to be nearer to the American one than to any other.

Lists of "Antarctic" plants always include the more or less circumpolar *Nertera depressa* (or *granadensis,* which is supposed by some to be the more correct name), but its Antarctic nature seems questionable. The genus is Indomalayan-Neo-Zelandic, with 1 species in China, 1 in Formosa, 1 or perhaps 2 in the Philippines, 1 in Australia, and 5 in New Zealand. Endemism is very pronounced in these species, in strong contrast to the peculiar behavior of *N. depressa,* which has been reported from Australia, Tasmania, New Zealand, Auckland, Campbell Island, Java (the Javanese form recently has been distinguished as a variety), the Philippine Islands, Hawaii, America from Mexico to Fuegia, the Falkland Islands, and Tristan da Cunha. A critical examination of a large body of material should be undertaken. We are likely to ask why none of the other species has attained a large range when each has edible berries which should offer the same facilities for dispersal. Perhaps there are biotic reasons for the many restricted areas.

I mention *Coprosma* with hesitation, but its luxuriant development in New Zealand compared to its very scanty representation in the Malayan region points toward a southern origin, and it is difficult to imagine a Tertiary Antarctic flora in which this genus was not represented. And, in a way, *Coprosma* may be called bicentric. There are 41 species in the New Zealand region, 7 in Australia with Tasmania, 2 in Norfolk Island, 3 in Lord Howe Island, 1 in the New Hebrides, 3 in Kermadec, 1 in Rarotonga, 1 in Fiji, 2 in Samoa, 4 in the Society Islands, 1 in Rapa, 1 in Tuamotu, 1 in Pitcairn, 2 in New Guinea, 1 in Borneo, 1 in Java, 17 in Hawaii (which is a remarkable secondary west Pacific center), and 2 in the Juan Fernandez Islands, but the genus is totally unknown on the American continent.

Diels[5] classifies *Coprosma* with his Australasian element in New Guinea. This component typically is absent from the South American continent—I point this out because 2 of the genera mentioned, *Coprosma* and *Halorrhagis,* belong to Juan Fernandez. I am unable to tell to which of the many species, Hawaiian or Neo-Zelandic, these two are most closely related. It is, of course, interesting that there are Australasian genera in Juan

Fernandez but not on the coast of Chile. However, I fail to see that there is any principal difference between these genera and, for example, *Lagenophora; Coprosma* and *Halorrhagis* very likely reached Juan Fernandez by way of land connected with what is now southern Chile. The definitive feature of all these occurrences is that the American representation is very weak as compared with the west Pacific one.

Another genus, *Coriaria,* might be quoted in this connection. *C. ruscifolia* used to be credited to both Chile and New Zealand, but now seems to be confined to America and replaced in New Zealand by *C. sarmentosa,* which extends to Warikauri (Chatham), Kermadec, and Tahiti. Another species is credited to tropical South America and New Zealand. When we consider the distribution of the genus in the northern hemisphere, where there are 4 species in an area extending from the Mediterranean region across Himalaya to Japan, and the occurrence of *Coriaria* in early Tertiary beds of Europe, the Antarctic nature of the family becomes very doubtful.

There are other genera for which an Antarctic-Polynesian distribution might be suggested. One of these is *Agrostis,* which has a Marquesas species that comes close to a Magellanian one.[2] However, we do not know these species or their positions within this largely Boreal genus well enough to discuss their possible history in the south.

If we leave the firmer ground of identical genera, some further examples of Antarctic-Polynesian distribution may be quoted. The *Dianella* group (Liliaceae) consists of 3 genera: *Dianella,* extending from the Mascarene Islands over Indomalaya-Australasia-Polynesia, *Stypandra* in Australia, and *Excremis* in South America. *Metrosideros,* an eminently western Pacific genus, reaches all high Pacific islands, has one stronghold in New

Zealand and another in Hawaii, and is represented in southern South America by the monotypical and closely related *Tepualia.* Of this genus, as of *Coprosma* and *Lagenophora,* we should speak of an Antarctic-Australasian element which reaches South America. There are several Antarctic-American genera, such as *Pernettya* and *Fuchsia,* which barely reach New Zealand.

The plants discussed above thrive in the warm-temperate, moist, and equable climate of the montane region in the monsoon and trade-wind zone. This is true of *Astelia, Lagenophora, Gunnera, Oreobolus, Uncinia, Nertera, Coprosma* and, to some degree, of *Acaena,* but many species of this genus live under quite different conditions. *Sophora,* without being a pronounced moisture-loving genus, shows great adaptability; this is especially true of the Hawaiian species. The conditions under which the ancestors of these plants lived in Antarctica are, of course, not known, but most likely they were not very different from those prevailing in the montane region within the tropics, on a lower level at higher latitudes, or even at sea level in subantarctic regions. Unfortunately, no representatives of this component are among the fossils known from Antarctic Tertiary beds, in which a subtropical and a more temperate (*Nothofagus*) flora are mixed (Dusén), a fact for which no entirely satisfactory explanation has yet been offered. In the present flora, both in Magellania and in New Zealand, *Nothofagus* species may be said to belong to the same belt or belts as our Antarcto-Pacific plants. Some of the ancestors of these latter certainly were fit to be preserved as fossils, and we hope to discover them some day. We may be quite sure that western Antarctica has not given up more than a small part of its treasures.

None of the genera spoken of here have what are called "impossible" fruits or seeds. Some, such as *Edwardsia,* cannot be said to show any special kind of adaptation. The wings of the pod, generally supposed to increase floating capacity, are absent in the two Juan Fernandez species; furthermore, experience shows that the ripe pods open on the tree, to which they are firmly attached, and discharge the seeds.[8, 14] According to Guppy, the seeds are buoyant. However, *Edwardsia* is not a seaside genus, and, although its seeds sometimes may be caught by the current, this so far has not led to an extension of specific range, because local endemism prevails throughout.

Gunnera has small, bright red drupes. In the Falkland Islands birds feed upon *G. magellanica* and thereby spread it. In Juan Fernandez, Chile, and Hawaii, where the Gunnerae are frequently seen growing on the banks of streams, the drupes are carried away by running water. *G. macrophylla* is probably distributed in the same way (at least in Java), but whether this habit has anything to do with the wide range of this species, I do not know; all the insular species of *Pangue* are restricted within a small area.

Astelia has a scarlet- or orange-colored berry and seeds with a hard but sometimes brittle testa. It is an established fact that birds eat the berries in Hawaii and New Zealand and very likely they do so wherever these plants grow, but endemism is absolute in this genus and, when a species is found in two remote stations, it is represented by different forms.

Coprosma, Nertera, and *Coriaria* have drupes. However, *Coprosma* shows pronounced local endemism. *Nertera,* if really the same species all over the southern hemisphere and beyond the equator, would strongly support the theory of endozoic oversea migration, but it is better not to draw far-reaching conclusions from the distribution of this genus; a careful revision of it will probably permit us to distinguish a number of endemic varieties or small species. Perhaps *Coriaria* will undergo the same metamorphosis, although its distribution by birds seems possible; the distances between the stations of *C. sarmentosa* are not very great, and part of the road may have been over land if there is any truth in the speculations of paleogeography.

Of the remaining genera, all of which have dry fruits, *Oreobolus* possesses no special facility for dispersal unless it be the small size of its fruits, which, I suppose, are carried about by birds frequenting the moist heaths where *Oreobolus* is at home. The range of *O. obtusangulus* in Andine America is very large. We have good reason to believe that, with the aid of birds, it reached the summit of Masafuera, together with a few more Magellanic species, under geographical conditions very similar to those of the present. However, in Hawaii we find a distinct endemic species living in utter geographical isolation.

The species of *Weinmannia* have, as a rule, a restricted range with pronounced endemism, but we have seen that the same species, in at least two instances, is credited to islands separated by wide expanses of ocean. The seeds are provided with long hairs and may be carried through the air for short distances; doubtless this is the normal way in which these plants are disseminated, but it is hard to tell what exceptional conditions enabled them to cover the distances between Rapa, Tahiti, and the Marquesas.

Acaena, Uncinia, and *Lagenophora* are particularly well adapted for epizoic dispersal. The achenes of *Acaena* have barbed bristles, and nobody denies that the introduced *A. argentea* has spread all over Masatierra because it adheres to man's clothes and to the furs of dogs, horses, and cattle. The indigenous species on the summit of Masafuera is not common, and its minute fruits perhaps do not attach themselves so easily to carriers; it is endemic, but close to two Magellanic species, and may be only an isolated part of one collective species. If this be right —and the behavior of another species, *A. adscendens,* strengthens the opinion—we conclude that oversea dispersal is a rare phenomenon; otherwise we should not find one uniform subspecies in South Georgia, another in Kerguelen, etc. We cannot very well believe that the seeds of a species A give rise to A only as long as they germinate in the island which it inhabits and that, if they are carried to other islands, they yield B or C or D instead of A; but we may believe that special types from a large and polymorphous population may become isolated in islands or on mountains where they are recognized as endemic varieties. Of course, the profoundly endemic species of *Astelia, Gunnera, Coprosma,* etc., require further explanation. Returning to *Acaena,* it is one thing to presume that *A. adscendens* obtained its present area in postglacial time with the aid of migrating birds, and another to conclude that the genus *Acaena* has conquered the southern hemisphere in the same manner, leaving relict endemic sections and species to bear witness to a traffic long suspended. Not rapid transportation across oceans, but slow migration over land of an already differentiated genus, with isolation and dying-out processes, accounts for this kind of endemism.

Uncinia resembles *Acaena.* The hooked rhachilla is an effective dispersal organ, and there is nothing supernatural in the way some species have traveled. However, the jump of *U. rupestris* from New Zealand to the Philippine Islands is quite astonishing and almost without parallel, matched only by the occurrence of *U. uncinata* in Hawaii.

Lagenophora has small adhesive achenes without any pappus, which suggests epizoic dispersal of such wide-ranging species as *L. Billardieri* and one or two subantarctic ones. Other species are much more local. We must not think that the various contrivances by which diaspores might become dispersed are useless or uninteresting simply because they do not accomplish transoceanic dispersal. They are not only useful, but also necessary. They enable a species to hold its ground and to reproduce within its present area, and help it to colonize new soil within reasonable distances. But as a rule they are not capable of greatly extending the area of the species, so long as biotic and other conditions remain unaltered, unless they are aided by man and his traffic. He carries the seeds of species involuntarily to the remotest places, where they spring up and thrive under conditions sometimes quite different. However, our experience does not show that they change and become new species.

The old Antarctic element in Polynesia, as represented in Hawaii and the Marquesas, is particularly interesting when affinity is not with Indomalaya-Australasia but with South America, though subantarctic rather than neotropical. *Acaena, Astelia, Gunnera* and, perhaps, *Edwardsia, Oreobolus,* and *Coprosma* have such affinities. A southeasterly road to Hawaii is thereby suggested. I have never felt inclined to believe that this affinity means floristic contact, but have preferred to think of each of these stations as end stations for migrations from Antarctica along either border of the Pacific. However, when all along the western road there are no relatives of the Hawaiian species, but such relatives are found in South America, we cannot refuse to consider the possibility of a more direct route. If there ever was such a road, its existence should perhaps be evidenced by the occurrence of a neotropical component in the Polynesian flora. This component does exist. And it will be difficult to discover roads of communication other than across the eastern Pacific.

J. D. Hooker, Diels, Setchell, Lam, Cockayne, and others speak, as I have here, of an Antarctic (or Paleantarctic) element, meaning that its original home should be sought in Antarctica. Miss Gibbs rejects this idea.[7] She notes "the relation between the mountain flora of North-West New Guinea and the so-called Antarctic flora" (p. 105), and gives a list of genera including *Oreobolus, Astelia, Acaena, Gunnera, Coprosma,* and *Lagenophora.* According to her ideas, however, this element is not at all Antarctic, but Papuan; the mountains of New Guinea she considers to be the focus of development and distribution of the "Antarctic" plants, justifying the term "Papuan austral-montane," instead of Antarctic, on the strength of both geological and meteorological data. The geological evidence would seem to be that "the present configuration of the New Guinea ranges dates from Tertiary time, the South American Cordillera according to present geological data was raised from below sea level in the Quaternary period, approximating to the epoch in which Tasmania assumed her present form."

Even if these statements were correct—the South American Cordillera is Tertiary and was the center of a glaciation contemporaneous with the Boreal Ice Age—the Antarctic floras still could have originated in the Antarctic continent. According to Miss Gibbs, this great land mass has been of no consequence whatever in the biological history of the southern hemisphere. The meteorological evidence implies that, in the strata above the trade wind, a poleward return wind blows. The wind is northwest and is supposed to have carried plant, also animal, life from its birthplace in New Guinea to southeastern Australia, Tasmania, New Zealand, and South America. This is a very bold theory indeed. To begin with, how many of the genera involved are wind-borne? Few, if any. *Oreobolus* and *Lagenophora* have not been found in New Guinea, but their existence there, which is not impossible, would make no difference. *Astelia, Acaena, Gunnera,* and *Coprosma* are represented by one species each. It is hard to believe that any of these genera were blown from New Guinea by a poleward wind, not only to New Zealand and the subantarctic islands, but also to Magellania, various islands in the southern Indian Ocean, and Africa, where they took the form of new sections and subgenera. It seems that Miss Gibbs was so struck by the wonderful development in New Guinea of another Antarctic (but not Polynesian) genus, *Drimys,* and by the discovery of the antitrade air currents, that she underrated the significance of the actual systematic structure and distribution of what I still prefer to call Antarctic genera. The force that, according to her opinion, carried them from New Guinea, would hardly have made them members of the Polynesian plant world.

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